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OF BATS
OF THE GENUS GLOSSOPHAGA**

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Series Editor
J. Knox Jones, Jr.

Published 30 July 1993

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Special Publications of The Museum are numbered serially and published on an irregular basis. Institutions interested in exchanging publications should address the Exchange Librarian at Texas Tech University.

ISSN 0149-1768

The ISBN number printed on the outside
back cover is incorrect. The correct number is
ISBN 0-89672-329-1

Texas Tech University Press
Lubbock, Texas USA

INTRODUCTION

Long-tongued bats of the genus *Glossophaga* are members of the New World family Phyllostomidae, and together with *Anoura*, *Brachyphylla*, *Choeroniscus*, *Choeronycteris*, *Erophylla*, *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, *Lionycteris*, *Lonchophylla*, *Monophyllus*, *Musonycteris*, *Phyllonycteris*, *Platalina*, and *Scleronycteris* comprise the predominantly pollen- and nectar-feeding tribe Glossophagini (Baker *et al.*, 1989). The geographic range of this genus extends from northern México (excluding most of the Mexican Plateau) southward to Paraguay and northern Argentina. Insular populations are known from the Tres Marías Islands, Jamaica, and islands adjacent to northern South America from Aruba eastward to Trinidad and Tobago, and hence northward (excluding Barbados) to St. Vincent. These bats occupy a wide variety of tropical habitats, from the arid coasts of western México and Perú to the rain forests of northwestern Colombia and central Brazil; they are unknown, however, from boreal elevations above 3000 meters in the Central American highlands or the Andes. They are gregarious and locally abundant, particularly in México and Central America where they are frequently among the most commonly collected bats.

The taxonomic history of *Glossophaga* is long and confusing. Pallas first described *Vespertilio soricinus* from Suriname in 1766. Subsequently, *V. soricinus* was referred to as *Phyllostoma soricinum* É. Geoffroy St.-Hilaire, 1810. The generic name *Glossophaga* was utilized first in 1818 by St.-Hilaire. Other specific names proposed in the early 19th Century for bats later regarded as representing *G. soricina* were *Glossophaga amplexicaudata* Spix, 1823, *Phyllophora nigra* Gray, 1844, and *Monophyllus leachii* Gray, 1944. The latter, long thought to be synonymous with *G. soricina*, recently has been determined to represent another species (Webster and Jones, 1980) of *Glossophaga*, a situation discussed beyond.

Several seemingly distinct taxa were described in the late 1800s and early 1900s. H. Allen (1896) described *G. villosa* from Venezuela, but later (1897) substituted the name *truei* for it because *villosa* was preoccupied. Merriam (1898) named *G. mutica* from the Tres Marías Islands, and Rehn (1902a) described *G. soricina antillarum* from Jamaica. Additionally, Miller (1898, 1900a, 1913a) described *G. longirostris* from northern Colombia, *G. elongata* from Curaçao, and *G. rostrata* from Grenada, respectively. The genus was reviewed by Miller (1913b) and divided into two complexes. His *soricina*-group included: *G. s. soricina* (Pallas) of northern South America (including *amplexicaudata*, *nigra*, and *truei*); *G. s. microtis*, a new subspecies from Paraguay; *G. s. mutica* Merriam of the Tres Marías Islands; *G. s. leachii* (Gray) from Middle America; *G. s. valens*, a new subspecies from coastal Perú; and *G. s. antillarum* Rehn of Jamaica. His *longirostris*-group included *G. l. longirostris* Miller from Colombia, *G. l. rostrata* Miller of Grenada, and *G. elongata* Miller of Curaçao.

Subsequent to Miller's revision, two similar taxa (both assigned to *Glossophaga soricina leachii*) were known from Central America (see Goodwin, 1934). One was smaller, darker, and had less protruding upper incisors than typical *leachii*. However, it was not considered specifically distinct because intermediates in size and pelage coloration were known. More confusion surrounding the identity and nomenclature of these taxa followed when Martínez and Villa-R. (1938) briefly described *G. morenoi* from Morelos, the type material of which subsequently was lost. Davis (1944) later described *G. soricina alticola* from Tlaxcala. It was contrasted from *leachii* as being larger, darker, and possessing less procumbent upper incisors, and was later recognized as a valid species by Baker (1967). Gardner (1962) described *G. commissarisi* from Chiapas, and distinguished it from *leachii* as being smaller, darker, and having less procumbent upper incisors. Gardner (1962), however, did not compare *commissarisi* with *alticola*, which still was regarded as a subspecies of *soricina* at that time.

The taxonomic history of bats of the genus *Glossophaga* from South America after Miller's revision also is complex. J. A. Allen (1916) described *G. apolinari* from Colombia, but Cabrera (1958) later reduced this taxon to subspecific status under *G. longirostris*. The type specimen, however, actually represents *Anoura cultrata* (Sanborn, 1933; Webster and Handley, 1986). Cabrera also synonymized *G. s. microtis* with *G. s. soricina*. Hummelinck (1940) reported on several specimens from Aruba, Curaçao, and Bonaire; and although one individual was reported as resembling *G. longirostris*, he allocated these specimens to *G. soricina* and synonymized *G. elongata* with *G. soricina*. Koopman (1958) later reexamined the individuals and correctly allocated them to *G. longirostris elongata*. Goodwin (1958) described *G. major* from Trinidad, but subsequently it was relegated to subspecific status under *G. longirostris* (Koopman, 1958).

Recently, Webster and Jones (1980) concluded that *Monophyllus leachii* Gray, 1844, actually represents what had been known previously as *G. alticola*; they placed the latter name in the synonymy of *G. leachii*, and designated the name *G. soricina handleyi* to replace the name *leachii* as applied to bats of the species *soricina* from the North American mainland. They also placed *G. morenoi* Martínez and Villa-R., 1938, in the synonymy of *G. leachii* following Villa-R. (1953, 1964, 1967). Alvarez (1966) and Urbano and Sánchez-H. (1983), however, considered *G. morenoi* a *nomen dubium* because the original description did not permit the species recognition, the diagnostic characters of the specimen designated as the neotype of *G. morenoi* by Villa-R. (1964) were not consistent with those of the holotype, and because four specimens associated with the type material, which had been lost but were subsequently rediscovered by Alvarez (1966), were assignable to *G. soricina*. Webster and Jones (1984a) described *G. mexicana brevirostris* from Morelos, and in doing so they noted (1984a:4) that "... the specimen (UNAM 7383) designated as the 'neotype' of *Glossophaga morenoi* by

Villa-R. (1964) actually represents *G. m. brevirostris* . . .” This prompted Gardner (1986) to consider *G. mexicana* a junior synonym of *G. morenoi*, an action that is discussed in more detail in the account of that species. Webster and Jones (1982) discovered that the distribution of *G. commissarisi* consisted of three disjunct populations, and named the race from northwestern México *G. c. hespera*; they (1983) also reported that *G. commissarisi* occurs in the Amazon lowlands of South America, and they (1987) named this race *G. c. bakeri*. *Glossophaga longirostris* was revised by Webster and Handley (1986); they recognized six races, two of which (*G. l. reclusa* and *G. l. campestris*) were unknown prior to that time.

The purpose of this study is to detail the evolution and systematics of bats of the genus *Glossophaga*. Nongeographic (individual and secondary sexual) and geographic variation indicate that five sibling species constitute the genus, and suggest that the relatively rapid climatic and habitat changes that took place during the Quaternary Period are responsible for the current patterns of distribution among the species. Five subspecies of *G. soricina* are herein recognized: *G. s. soricina* from Colombia (east of the Andes), Venezuela, Trinidad, and Guianas southward to northern Argentina; *G. s. handleyi* from Sonora and Tamaulipas southward to western Colombia; *G. s. mutica* from the Tres Marías Islands; *G. s. antillarum* from Jamaica; and *G. s. valens* from western Ecuador and Perú. The monotypic *G. leachii* extends along the Pacific versant of Middle America from Colima and Jalisco southeastward to central Costa Rica. Three subspecies of *G. commissarisi* are recognized—*G. c. commissarisi* from Veracruz and Oaxaca southeastward to Panamá, *G. c. hespera* from Sinaloa southward to Colima, and *G. c. bakeri* from the upper Amazon Basin. Two subspecies of *G. morenoi* are recognized—*G. m. morenoi* from Michoacán, Morelos, and Puebla southeastward to western Oaxaca, and *G. m. mexicana* from eastern Oaxaca and western Chiapas. Six subspecies of *G. longirostris* are recognized: *G. l. longirostris* from northern Colombia and northwestern Venezuela; *G. l. elongata* from Aruba, Curaçao, and Bonaire; *G. l. rostrata* from St. Vincent, the Grenadines, Grenada, and Tobago; *G. l. reclusa* from the upper Magdalena River Valley; *G. l. campestris* from the llanos of Venezuela, Guayana, and adjacent Brazil; and *G. l. major* from Trinidad, the coastal areas of northern Venezuela, and the llanos of Colombia.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

This study is based on examination of 6345 specimens of *Glossophaga*, most of which were conventional skins accompanied by skulls; however, some consisted of skulls and postcranial skeletons, skulls without accompanying skins, or specimens preserved in fluid (from some of which skulls had been extracted). All data on labels associated with specimens were recorded. In addition, molt patterns were mapped for each individual found to have been in the process of molt. All measurements used in morphometric analyses were taken from adults (completely fused

phalangeal epiphyses and well-ossified cranial sutures) with dial calipers, calibrated to a twentieth of a millimeter and recorded to a tenth of a millimeter (mm). Due to inconsistency in measuring specimens by collectors in the field, there is an increased variation associated with conventional external measurements (Sumner, 1927; Van Gelder, 1959) as opposed to those taken in the laboratory by a single researcher. Therefore, the only external characters critically analyzed were those measured by me—length of forearm and length of the third, fourth, and fifth metacarpals. Also, 12 cranial measurements and 10 multistate qualitative characteristics were recorded for each specimen, as was weight if available.

Length of forearm.—Greatest distance between proximal extremity of sesamoid bone and distal extremity of carpals when wing is folded.

Length of third metacarpal.—Greatest distance when wing is folded.

Length of fourth metacarpal.—Greatest distance when wing is folded.

Length of fifth metacarpal.—Greatest distance when wing is folded.

Weight.—From specimen label, in grams.

Greatest length of skull.—Greatest distance from posteriormost projection of occiput to anteriormost projection of upper incisors.

Condylbasal length.—Least distance from posteriormost projection of exoccipital condyles to anteriormost projection of premaxillae.

Zygomatic breadth.—Greatest width across zygomatic arches perpendicular to longitudinal axis of cranium.

Length of rostrum.—Least distance (straight line) from anteriormost projection of premaxillae to anteriormost projection of temporal fossa at jugal-maxilla suture.

Mastoid breadth.—Greatest width across mastoidal processes perpendicular to longitudinal axis of cranium.

Interorbital breadth.—Least distance across interorbital constriction perpendicular to longitudinal axis of cranium and anterior to postorbital constriction.

Breadth of braincase.—Greatest width across parietals dorsal to auditory meatus and perpendicular to longitudinal axis of cranium.

Depth of braincase.—Least distance from dome of cranium to a straight line connecting pterygo-palatine (laterad to presphenoid) and basioccipital.

Length of maxillary toothrow.—Greatest distance from anteriormost projection of canine to posteriormost projection of third molar.

Length of c-m3 mandibular toothrow.—Greatest distance from anteriormost projection of canine to posteriormost projection of third molar.

Width across molars.—Greatest distance across palate between labialmost projection of upper molars.

Mandibular length.—Greatest distance from anteriormost projection of lower incisors to posteriormost projection of both dentary condyles (not taken when rami were disarticulated).

Pelage coloration.—From pale (1) on dorsum (albinos excluded) to dark (8).

Pterygoid alae.—Absent (1), modestly developed or present only on one side (2), present and well developed on both sides (3).

Presphenoid ridge.—Incomplete (1), complete but not prominent (2), complete and prominent (3).

Lower incisors.—Small and spaced (1), small and paired (2), medium-sized and paired or medium in size but not in contact (3), large and in contact (4).

Upper incisor angle.—Greatly procumbent (1), procumbent (2), not noticeably procumbent (3).

Upper incisor size.—Not equal (1), subequal (2), equal (3).

Basisphenoid pits.—Shallow (1), moderately deep (2), deep (3).

P3:P4 bulk.—Not equal (1), subequal (2), equal (3).

Rostral slope.—Continuous rise from rostrum to braincase (1), braincase rising gradually from rostrum (2), braincase rising moderately from rostrum (3), braincase rising abruptly from rostrum.

Posterior palatine process.—Absent (1), poorly developed (2), moderately developed (3), greatly developed and falcate (4).

The grouping procedure for analyses of nongeographic variation was based primarily on sample size; populations that were well represented from a single locality were analyzed separately. Grouping for analyses of geographic variation was based on geographic proximity (with due consideration of physiographic features) and on sample size. Thus, those individuals constituting an OTU (Operational Taxonomic Unit) were from isolated populations or contiguous geographic areas. For example, insular populations were treated separately from those on the adjacent mainland and populations that occupied habitats divided by mountain ranges were treated as distinct OTUs, whereas western Amazonian Brazil was treated as a single OTU, in order to achieve an adequate sample size, because no known physio-graphic barrier exists in that region.

Pelage coloration was assessed numerically by comparing each individual with four specimens selected from the collection the The Museum, Texas Tech University, which were numbered one (pale), three, five, and seven (dark). The color of the four specimens used in these comparisons as well as representative individuals of all species of *Glossophaga* deposited in the National Museum of Natural History was determined under an Exam-O-Lite using Ridgway (1912).

For the analysis of genic variability, tissues (liver, heart, and kidney) were removed from specimens immediately after sacrifice and frozen in liquid nitrogen. Techniques for tissue preparation, electrophoresis, and biochemical staining were essentially those described by Selander *et al.* (1971). Seventeen isozymes were assayed including the presumptive loci Malate dehydrogenase—1, 2 (Mdh—1,2), Lactate dehydrogenase—1, 2 (Ldh—1,2), Isocitrate dehydrogenase—1, 2 (Idh—1,2), Albumin (Alb), Mannose-6-phosphate isomerase (Mpi), Phosphoglucosmutase—1, 2 (Pgm—1,2), Glutamate oxalate transaminase—1, 2 (Got—1,2), α -Glycerophosphate dehydrogenase (α -Gpd), Alcohol dehydrogenase (Adh), Indophenyl oxidase (Ipo), and Peptidase—1, 2 (Pep—1,2). The substrates used to resolve the peptidases were Glycyl-L-leucine (Pep-1) and DL-Leucylglycylglycine (Pep-2). Outgroups (*Mono-phyllus*, *Leptonycteris*, *Choeronycteris*, and *Lonchophylla*) were used to determine pleisiomorphies and the evolutionary direction of character states. Rogers' similarity values (Rogers, 1972) were calculated from the allozyme data, and a similarity phenogram between OTUs was generated from the similarity matrix using the NT-SYS program (Sokal and Rohlf, 1981).

Statistical procedures were performed on the IBM 360/50 computer at Texas Tech University, the IBM 378/158 computer at the University of Oklahoma, and Amdahl 470/V8 computer at the Triangle University Computing Center (Triangle Park, North Carolina). Many statistical packages require complete data matrices; therefore, values of missing characters were estimated by linear regression with SAS programs (Barr *et al.*, 1979) provided no more than two characters were missing for any individual. The character that had the highest correlation ($R^2 > 0.75$, based on the pooled sample for each species) with the missing measurement was used in the regression equation to provide the best least-squares estimate of that missing value. Univariante analyses of quantitative characters yielded standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) using SAS packages, and employed single classification analysis of variance (*F*-test, significance level 0.05) to test for significant differences between or among means of OTUs. When means were significantly different, Gabriel's (1964) Sums of Squares Simultaneous Test Procedure (SS-STP) was used to determine maximally nonsignificant subsets. Multivariate analyses were performed on all morphometric data using NT-SYS programs. Matrices of Pearson's product-moment correlations were computed and phenetic distance coefficients were derived from standardized character values. Characters were clustered using UPGMA (unweighted pair-group method using arithmetic averages) on the correlation and distance matrices and a phenogram was generated for each. A character correlation matrix was computed and the first four principal components were extracted; two-dimensional projections of the OTUs onto the first four principal components were made. All original data are on file and may be obtained from the author on request.

Special thanks are extended to the following institutions and curators who made material in their care available to me. Abbreviations preceding the names of institutions are used in the accounts beyond to identify the source of specimens.

- AMNH—American Museum of Natural History, New York (Karl F. Koopman);
- ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia (Charles L. Smart, Jr.);
- CAS—California Academy of Science, San Francisco (Robert T. Orr);
- CMNH—Carnegie Museum of Natural History, Pittsburg (Hugh H. Genoways);
- FMNH—Field Museum of Natural History, Chicago (Robert M. Timm);
- KU—Museum of Natural History, University of Kansas, Lawrence (Robert S. Hoffmann);
- LSU—Museum of Zoology, Louisiana State University, Baton Rouge (Mark S. Hafner);
- MCZ—Museum of Comparative Zoology, Harvard University, Cambridge (John A. W. Kirsch);
- MSB—Museum of Southwestern Biology, University of New Mexico, Albuquerque (James S. Findley and Terry L. Yates);
- MSU—The Museum, Michigan State University, East Lansing (Rollin H. Baker and Donald O. Straney);
- MVZ—Museum of Vertebrate Zoology, University of California, Berkeley (William Z. Lidicker, Jr., and James L. Patton);

- OU—Stoal Museum of Science and History, University of Oklahoma, Norman (J. Keever Greer);
- ROM—Royal Ontario Museum, Toronto (Randolph L. Peterson and James R. Tamsitt);
- TCWC—Texas Cooperative Wildlife Collection, Texas A&M University, College Station (David J. Schmidly);
- TTU—The Museum, Texas Tech University, Lubbock (Robert J. Baker);
- UA—University of Arizona, Tucson (E. Lendell Cockrum);
- UCV—Universidad Central de Venezuela (Carlos J. Naranjo and Carlos Machado);
- UMMZ—Museum of Zoology, University of Michigan, Ann Arbor (Philip Myers);
- UNAM—Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F. (Bernardo Villa-R.);
- USNM—National Museum of Natural History, including the Biological Surveys Collection, Washington, D. C. (Charles O. Handley, Jr., and Don E. Wilson).

It is appropriate at this point to make a general comment about the format followed in the species accounts. Species are listed alphabetically, as are subspecies within each species. Statements regarding the phylogenetic relationships among subspecies or species are discussed where warranted. One problem that I could not resolve concerned the authenticity of specific identifications published prior to about 1970, the time when it became apparent that at least three species (and not the ubiquitous "*Glossophaga soricina leachii*") inhabited parts of México and Central America. Therefore, the results of investigations published before 1970 and in which reference is made to *G. soricina leachii* were omitted from this study unless I examined voucher specimens or was convinced that *G. soricina* only occurred in the area from which the specimens were secured. As a result, "Selected additional records" follow the list of specimens examined in the account of *G. soricina handleyi*, listing only localities from where I feel certain that the specific identifications are accurate. I have a similar section in the account of *G. s. soricina*, because representative localities only were picked from the numerous publications making reference to that bat. In all other accounts, however, I have listed "Additional records" after the list of specimens examined.

I am deeply indebted to J. Knox Jones, Jr., Chairman of my Advisory Committee, for his invaluable guidance and assistance during this investigation. Preliminary work on the genus *Glossophaga* by Jones and James Dale Smith, then at the University of Kansas, the results of which were made available to me in unpublished form, simplified certain aspects of the study. Robert J. Baker, Dillard C. Carter, Charles O. Handley, Jr., and M. Kent Rylander contributed significantly as members of my Advisory Committee, and the late Robert L. Packard assisted me as an advisor and member of the Committee until his untimely death. Additional gratitude is extended to Robert D. Owen, then at the University of Oklahoma, for his advice concerning the statistical techniques employed herein, and to other graduate students and professors at Texas Tech University and other institutions who willingly discussed with me the problem at hand. Michael L. Arnold, Robert J. Baker, Linda J.

Barkley, Richard K. Barnett, Anette J. Carlisle, Hugh H. Genoways, Michael W. Haiduk, Rodney L. Honeycutt, Lynn W. Robbins, and R. Laurie Robbins assisted in the collection of specimens and tissues used in the genic analysis, and Michael L. Arnold assisted with the electrophoretic studies. Adam Krzanowski provided photographs and comments about the hair structure of *Glossophaga*. Kim A. Parham continually provided cheerful clerical assistance. I would like to extend a special thanks to Don, Peggy, and Kerry Webster, and my wife, Penny, for their constant support and encouragement throughout this study. This research was supported in part by grants from the American Museum of Natural History (Theodore Roosevelt Memorial Fund) and the National Science Foundation (DEB-76-20580 and DEB-80-04293 to Robert J. Baker), and stipends from the Graduate School and Department of Biological Sciences of Texas Tech University; computer time was provided by the Institute of Museum Research (Texas Tech University), Department of Zoology (University of Oklahoma), and Department of Biological Sciences (University of North Carolina at Wilmington).

NONGEOGRAPHIC VARIATION

In any systematic investigation, it is imperative to partition the total variation for each taxon into components that represent recognizable subunits such as variation due to age, secondary sexual variation, individual variation irrespective of age and sex, and an error variation associated with the investigator (Straney, 1978). Non-geographic variation classically has been quantified as the coefficient of variation (CV); however, in some past systematic studies no effort was made to take account of other sources of variation and the CV thus becomes spurious.

In this investigation, every attempt has been made to partition variation into categories that best explain the total variation within each taxon. Ontogenetic variation was not examined because only adults were measured. Secondary sexual variation was examined prior to the assessment of individual variation to minimize the interaction between the two. Some slight error on my part was inevitable and was estimated at 1.2 percent by measuring a series of specimens on two separate occasions (11 months apart).

Secondary Sexual Variation

Adult males were tested against adult females for each species using single classification ANOVA to determine if the sexes were significantly different in size. Weight was not included in these analyses. The results of these tests are discussed below and shown in Table 1.

Glossophaga commissarisi.—Females were found to be significantly larger than males in two (length of rostrum and mandibular length) of the 16 measurements tested. Females averaged larger than males in nine other measurements (length of forearm, length of third metacarpal, length of fourth metacarpal, length of fifth

TABLE 1.—*Secondary sexual variation in external and cranial measurements in five species of Glossophaga. Specimens used in the analyses include: G. commissarisi from ca. Tonalá, Chiapas; G. leachii from Teloloapan, Guerrero; G. longirostris from Curaçao; G. morenoi from the Pacific lowlands of eastern Oaxaca; and G. soricina from ca. Balao, Ecuador. Statistics include samples size, mean, two standard deviations, range, coefficient of variation, and F and probability values. Means for males and females that are significantly different at $P \leq 0.05$ are marked with an asterisk, but those in which no significant difference was found are marked ns.*

Measurements and sex	N	Mean \pm 2 SD	Range	CV	F P \leq	
<i>Glossophaga commissarisi</i>						
Length of forearm						
Male	19	33.48 \pm 2.28	(31.1–35.1)	3.41	1.52	ns
Female	21	33.94 \pm 2.36	(32.0–36.6)	3.48	0.2252	
Length of third metacarpal						
Male	19	33.49 \pm 2.41	(31.7–35.4)	3.60	0.03	ns
Female	21	33.55 \pm 2.13	(31.6–36.0)	3.18	0.8722	
Length of fourth metacarpal						
Male	19	31.38 \pm 2.20	(29.7–33.5)	3.50	0.25	ns
Female	21	31.54 \pm 1.81	(29.5–33.6)	2.86	0.6182	
Length of fifth metacarpal						
Male	19	30.90 \pm 2.44	(28.8–33.2)	3.95	0.02	ns
Female	21	30.95 \pm 1.99	(28.5–32.9)	3.22	0.8821	
Greatest length of skull						
Male	19	19.99 \pm 0.88	(19.3–21.0)	2.20	0.00	ns
Female	21	20.00 \pm 0.53	(19.5–20.5)	1.31	0.9631	
Condylbasal length						
Male	19	18.27 \pm 0.90	(17.2–19.1)	2.46	0.76	ns
Female	21	18.37 \pm 0.58	(17.8–19.0)	1.57	0.3893	
Zygomatic breadth						
Male	18	9.46 \pm 0.55	(9.0–10.1)	2.88	1.73	ns
Female	19	9.36 \pm 0.40	(9.1–9.9)	2.15	0.1966	
Length of rostrum						
Male	19	7.73 \pm 0.41	(7.3–8.0)	2.62	4.28	*
Female	21	7.85 \pm 0.30	(7.5–8.1)	1.92	0.0455	
Mastoid breadth						
Male	19	8.99 \pm 0.46	(8.7–9.4)	2.55	0.24	ns
Female	21	8.97 \pm 0.24	(8.8–9.2)	1.34	0.6259	
Interorbital breadth						
Male	19	4.01 \pm 0.26	(3.8–4.3)	3.21	0.10	ns
Female	21	4.02 \pm 0.28	(3.8–4.3)	3.42	0.7548	
Breadth of braincase						
Male	19	8.48 \pm 0.33	(8.2–8.9)	1.94	0.34	ns
Female	21	8.46 \pm 0.26	(8.3–8.8)	1.52	0.5632	
Depth of braincase						
Male	19	6.95 \pm 0.27	(6.7–7.2)	1.94	2.38	ns
Female	21	6.89 \pm 0.28	(6.6–7.1)	2.02	0.1312	
Length of maxillary toothrow						
Male	18	6.76 \pm 0.30	(6.5–7.0)	2.22	0.44	ns
Female	21	6.79 \pm 0.25	(6.5–7.0)	1.86	0.5107	

TABLE 1.—Continued.

Measurements and sex	N	Mean \pm 2 SD	Range	CV	F P \leq	
Length of mandibular toothrow						
Male	18	7.19 \pm 0.27	(7.0–7.4)	1.88	0.12	ns
Female	21	7.18 \pm 0.37	(6.8–7.5)	2.57	0.7299	
Width across molars						
Male	18	5.45 \pm 0.33	(5.1–5.7)	3.04	0.03	ns
Female	21	5.46 \pm 0.22	(5.2–5.6)	1.97	0.8721	
Mandibular length						
Male	19	12.71 \pm 0.35	(12.5–13.1)	1.36	7.03	*
Female	20	12.87 \pm 0.38	(12.6–13.3)	1.48	0.0117	
<i>Glossophaga leachii</i>						
Length of forearm						
Male	13	36.59 \pm 1.65	(35.4–38.0)	2.25	2.85	ns
Female	6	37.25 \pm 1.40	(36.5–38.2)	1.88	0.1098	
Length of third metacarpal						
Male	13	36.33 \pm 2.16	(34.7–39.0)	2.97	1.72	ns
Female	6	37.02 \pm 2.02	(35.7–38.2)	2.73	0.2065	
Length of fourth metacarpal						
Male	14	33.56 \pm 1.72	(32.3–35.3)	2.57	5.47	*
Female	6	34.62 \pm 2.13	(33.6–36.3)	3.08	0.0311	
Length of fifth metacarpal						
Male	14	32.29 \pm 1.60	(31.0–34.0)	2.48	4.96	*
Female	6	33.25 \pm 2.12	(31.9–34.4)	3.19	0.0389	
Greatest length of skull						
Male	15	20.38 \pm 0.49	(20.1–20.7)	1.21	1.71	ns
Female	6	20.57 \pm 0.81	(20.2–21.3)	1.96	0.2063	
Condylobasal length						
Male	15	18.80 \pm 0.73	(17.8–19.3)	1.93	2.20	ns
Female	5	19.08 \pm 0.75	(18.7–19.7)	1.98	0.1555	
Zygomatic breadth						
Male	12	9.51 \pm 0.41	(9.1–9.8)	2.17	0.04	ns
Female	3	9.53 \pm 0.42	(9.3–9.7)	2.18	0.8543	
Length of rostrum						
Male	16	8.03 \pm 0.44	(7.5–8.4)	2.71	2.03	ns
Female	6	8.17 \pm 0.35	(7.9–8.4)	2.14	0.1698	
Mastoid breadth						
Male	12	9.15 \pm 0.26	(8.9–9.4)	1.44	3.81	ns
Female	4	8.98 \pm 0.44	(8.7–9.2)	2.47	0.0712	
Interorbital breadth						
Male	14	3.99 \pm 0.28	(3.7–4.2)	3.53	0.00	ns
Female	6	3.98 \pm 0.29	(3.7–4.1)	3.70	0.9731	
Breadth of braincase						
Male	13	8.71 \pm 0.35	(8.4–9.0)	2.01	0.49	ns
Female	5	8.64 \pm 0.41	(8.3–8.8)	2.40	0.4943	

TABLE 1.—Continued.

Measurements and sex	N	Mean ± 2 SD	Range	CV	F P≤	
Depth of braincase						
Male	14	7.09±0.68	(6.0–7.4)	4.82	0.00	ns
Female	6	7.08±0.48	(6.8–7.5)	3.39	0.9879	
Length of maxillary toothrow						
Male	15	6.94±0.39	(6.6–7.3)	2.82	0.29	*
Female	6	7.15±0.17	(7.1–7.3)	1.17	0.0214	
Length of mandibular toothrow						
Male	15	7.36±0.35	(7.0–7.7)	2.40	1.46	ns
Female	6	7.45±0.11	(7.4–7.5)	0.74	0.2414	
Width across molars						
Male	15	5.67±0.34	(5.4–5.9)	2.96	0.78	ns
Female	6	5.73±0.24	(5.6–5.9)	2.11	0.3895	
Mandibular length						
Male	15	13.15±0.40	(12.7–13.4)	1.52	3.99	ns
Female	5	13.34±0.18	(13.2–13.4)	0.67	0.0611	
<i>Glossophaga longirostris</i>						
Length of forearm						
Male	13	36.65±1.73	(35.3–38.1)	2.35	5.86	*
Female	14	37.41±1.54	(36.4–38.9)	2.06	0.0231	
Length of third metacarpal						
Male	13	37.72±1.84	(36.3–39.3)	2.44	0.58	ns
Female	14	37.99±1.84	(36.8–39.7)	2.42	0.4535	
Length of fourth metacarpal						
Male	13	34.31±1.42	(33.2–35.7)	2.08	0.89	ns
Female	14	34.61±1.84	(33.2–36.1)	2.65	0.3553	
Length of fifth metacarpal						
Male	13	33.75±1.83	(32.0–35.1)	2.71	1.55	ns
Female	14	34.15±1.54	(33.0–35.8)	2.26	0.2254	
Greatest length of skull						
Male	14	23.39±0.72	(22.5–23.9)	1.54	10.60	*
Female	14	23.82±0.70	(23.3–24.6)	1.47	0.0032	
Condylobasal length						
Male	14	21.72±0.76	(20.9–22.2)	1.74	9.20	*
Female	14	22.14±0.69	(21.7–22.6)	1.55	0.0054	
Zygomatic breadth						
Male	12	9.41±0.31	(9.2–9.7)	1.66	0.29	ns
Female	14	9.44±0.34	(9.2–9.8)	1.80	0.5969	
Length of rostrum						
Male	14	9.29±0.48	(8.7–9.6)	2.58	7.21	*
Female	14	9.51±0.35	(9.2–9.7)	1.87	0.0124	
Mastoid breadth						
Male	14	8.89±0.36	(8.5–9.2)	2.02	8.30	*
Female	14	9.05±0.23	(8.9–9.2)	1.28	0.0079	

TABLE 1.—Continued.

Measurements and sex	N	Mean ± 2 SD	Range	CV	F P≤	
Interorbital breadth						
Male	14	4.23±0.31	(4.0–4.6)	3.64	0.00	ns
Female	14	4.23±0.20	(4.1–4.4)	2.35	1.0000	
Breadth of braincase						
Male	14	8.54±0.38	(8.3–8.8)	2.24	0.18	ns
Female	14	8.57±0.34	(8.3–8.8)	1.96	0.6780	
Depth of braincase						
Male	14	6.65±0.36	(6.3–7.0)	2.69	0.05	ns
Female	14	6.66±0.29	(6.4–6.9)	2.17	0.8180	
Length of maxillary toothrow						
Male	14	7.92±0.39	(7.5–8.1)	2.44	4.00	ns
Female	14	8.06±0.33	(7.8–8.4)	2.05	0.0560	
Length of mandibular toothrow						
Male	14	8.41±0.46	(7.9–8.7)	2.71	0.14	ns
Female	14	8.44±0.34	(8.1–8.8)	2.01	0.7100	
Width across molars						
Male	14	5.90±0.37	(5.4–6.1)	3.12	0.06	ns
Female	14	5.89±0.25	(5.7–6.1)	2.09	0.8111	
Mandibular length						
Male	14	15.06±0.67	(14.5–15.5)	2.24	3.60	ns
Female	14	15.26±0.46	(14.9–15.7)	1.51	0.0688	
<i>Glossophaga morenoi</i>						
Length of forearm						
Male	21	34.58±1.52	(33.5–36.5)	2.19	1.46	ns
Female	12	34.89±1.22	(33.6–35.8)	1.75	0.2353	
Length of third metacarpal						
Male	21	34.85±1.86	(33.4–36.4)	2.66	0.16	ns
Female	12	34.72±1.71	(33.0–36.0)	2.46	0.6912	
Length of fourth metacarpal						
Male	21	32.05±1.66	(30.8–33.8)	2.59	0.00	ns
Female	21	32.05±1.66	(30.5–33.1)	2.60	0.9937	
Length of fifth metacarpal						
Male	21	31.30±1.65	(30.0–32.7)	2.63	0.45	ns
Female	12	31.49±1.47	(30.1–32.9)	2.33	0.5091	
Greatest length of skull						
Male	19	22.02±0.75	(21.4–22.7)	1.71	0.06	ns
Female	12	21.98±0.59	(21.3–22.4)	1.34	0.8018	
Condylobasal length						
Male	19	20.44±0.83	(19.8–21.5)	2.03	0.97	ns
Female	12	20.57±0.47	(20.1–20.9)	1.14	0.3331	
Zygomatic breadth						
Male	18	9.64±0.43	(9.1–10.1)	2.25	4.86	*
Female	10	9.45±0.43	(9.0–9.7)	2.30	0.0366	

TABLE 1.—Continued.

Measurements and sex	N	Mean ± 2 SD	Range	CV	F P≤	
Length of rostrum						
Male	21	9.03±0.43	(8.7–9.4)	2.36	1.45	ns
Female	12	9.13±0.41	(8.7–9.4)	2.25	0.2372	
Mastoid breadth						
Male	19	9.06±0.32	(8.8–9.5)	1.78	1.21	ns
Female	12	8.98±0.43	(8.6–9.4)	2.41	0.2811	
Interorbital breadth						
Male	20	4.20±0.32	(3.8–4.5)	3.78	1.62	ns
Female	12	4.13±0.33	(3.8–4.3)	4.02	0.2132	
Breadth of braincase						
Male	20	8.69±0.28	(8.4–9.0)	1.64	4.42	*
Female	12	8.57±0.34	(8.2–8.8)	2.01	0.0439	
Depth of braincase						
Male	19	6.85±0.33	(6.5–7.2)	2.40	1.08	ns
Female	12	6.91±0.30	(6.7–7.2)	2.18	0.3081	
Length of maxillary toothrow						
Male	21	7.73±0.29	(7.4–8.0)	1.88	4.25	*
Female	12	7.84±0.32	(7.5–8.0)	2.07	0.0477	
Length of mandibular toothrow						
Male	21	8.19±0.31	(8.0–8.5)	1.86	0.62	ns
Female	12	8.23±0.38	(7.8–8.4)	2.34	0.4387	
Width across molars						
Male	21	5.76±0.27	(5.4–6.0)	2.37	0.64	ns
Female	12	5.72±0.29	(5.5–6.0)	2.57	0.4306	
Mandibular length						
Male	20	14.41±0.59	(14.0–15.1)	2.05	2.81	ns
Female	12	14.59±0.60	(13.9–15.0)	2.06	0.1044	
<i>Glossophaga soricina</i>						
Length of forearm						
Male	9	35.47±1.33	(34.4–36.3)	1.88	10.75	*
Female	3	36.90±1.22	(36.5–37.6)	1.65	0.0083	
Length of third metacarpal						
Male	9	35.40±1.56	(33.6–36.5)	2.21	1.99	ns
Female	3	36.20±2.16	(35.0–37.1)	2.99	0.1882	
Length of fourth metacarpal						
Male	9	32.50±1.41	(31.2–33.5)	2.17	3.82	ns
Female	3	33.57±2.34	(32.3–34.6)	3.48	0.0793	
Length of fifth metacarpal						
Male	9	31.47±1.28	(30.2–32.5)	2.04	4.43	ns
Female	3	32.57±2.39	(31.2–33.4)	3.66	0.0616	
Greatest length of skull						
Male	10	22.08±0.51	(21.7–22.4)	1.17	5.04	*
Female	10	22.41±0.77	(21.7–23.1)	1.73	0.0376	

TABLE 1.—*Continued.*

Measurements and sex	N	Mean ± 2 SD	Range	CV	F P≤	
Condylobasal length						
Male	10	20.39±0.52	(20.0–20.7)	1.28	9.32	*
Female	10	20.82±0.72	(20.2–21.3)	1.74	0.0068	
Zygomatic breadth						
Male	10	9.61±0.33	(9.4–9.9)	1.73	0.58	ns
Female	10	9.55±0.37	(9.3–9.8)	1.93	0.4543	
Length of rostrum						
Male	10	8.84±0.36	(8.6–9.1)	2.01	10.42	*
Female	10	9.10±0.37	(8.9–9.5)	2.01	0.0047	
Mastoid breadth						
Male	10	9.19±0.22	(9.0–9.4)	1.20	0.26	ns
Female	10	9.15±0.44	(8.8–9.5)	2.43	0.6164	
Interorbital breadth						
Male	10	4.27±0.27	(4.1–4.5)	3.13	0.33	ns
Female	10	4.24±0.19	(4.1–4.4)	2.28	0.5724	
Breadth of braincase						
Male	10	8.58±0.20	(8.5–8.7)	1.07	0.33	ns
Female	10	8.63±0.52	(8.2–9.1)	2.99	0.5714	
Depth of braincase						
Male	10	7.04±0.23	(6.9–7.2)	1.67	0.12	ns
Female	10	7.01±0.50	(6.6–7.5)	3.59	0.7364	
Length of maxillary toothrow						
Male	10	7.54±0.38	(7.3–7.9)	2.52	8.54	*
Female	9	7.81±0.43	(7.6–8.3)	2.75	0.0095	
Length of mandibular toothrow						
Male	10	8.00±0.37	(7.7–8.3)	2.28	5.72	*
Female	9	8.22±0.44	(8.0–8.7)	2.70	0.0286	
Width across molars						
Male	10	5.83±0.19	(5.7–6.0)	1.63	6.08	*
Female	10	5.69±0.30	(5.5–6.0)	2.68	0.0239	
Mandibular length						
Male	10	14.25±0.51	(13.4–14.6)	1.79	6.67	*
Female	9	14.56±0.52	(14.1–15.0)	1.79	0.0194	

metacarpal, greatest length of skull, condylobasal length, interorbital breadth, length of maxillary toothrow, and width across molars). Males averaged larger than females in the five remaining measurements (zygomatic breadth, mastoid breadth, breadth of braincase, depth of braincase, and length of mandibular toothrow).

Glossophaga leachii.—Females were significantly larger than males in three (length of fourth metacarpal, length of fifth metacarpal, and length of maxillary toothrow) of the 16 measurements tested. Females averaged larger than males in nine others (length of forearm, length of third metacarpal, greatest length of skull,

condylobasal length, zygomatic breadth, length of rostrum, length of mandibular toothrow, width across molars, and mandibular length), whereas males averaged larger than females in four measurements (mastoid breadth, interorbital breadth, breadth of braincase, and depth of braincase).

Glossophaga longirostris.—Females were found to be significantly larger than males in five (length of forearm, greatest length of skull, condylobasal length, length of rostrum, and mastoid breadth) of the 16 measurements tested. Females averaged larger than males in nine of the remaining measurements (length of third, fourth, and fifth metacarpals, zygomatic breadth, breadth of braincase, depth of braincase, length of maxillary and mandibular toothrows, and mandibular length), whereas males averaged larger than females in two (interorbital breadth and width across molars).

Glossophaga morenoi.—Females were significantly larger than males only in length of maxillary toothrow, but averaged larger than males in eight other of the 16 measurements (length of forearm, length of fourth metacarpal, length of fifth metacarpal, condylobasal length, length of rostrum, depth of braincase, length of mandibular toothrow, and mandibular length). Males were found to be significantly larger than females in two (zygomatic breadth and breadth of braincase) measurements and averaged larger than females in five (length of third metacarpal, greatest length of skull, mastoid breadth, interorbital breadth, and width across molars).

Glossophaga soricina.—Females were found to be significantly larger than males in seven (length of forearm, greatest length of skull, condylobasal length, length of rostrum, length of maxillary toothrow, length of mandibular toothrow, and mandibular length) of the 16 measurements tested, and averaged larger than males in another four (length of third, fourth, and fifth metacarpals, and breadth of braincase). Males were significantly larger than females in width across molars and averaged larger than females in zygomatic breadth, mastoid breadth, interorbital breadth, and depth of braincase.

Conclusions.—Females were found to be significantly larger than males in 22.5 percent of the measurements tested and averaged larger than males in another 48.8 percent of the measurements. Taddei (1975) found female *G. soricina* to be significantly larger than males in four of 17 external measurements (head and body length, length of forearm, length of fourth metacarpal, and length of fifth metacarpal) and two of 15 cranial measurements (molar length and length of mandibular toothrow). He found males to be significantly larger than females in five cranial measurements (breadth across canines, zygomatic breadth, breadth of braincase, mastoid breadth, and depth of braincase). Willig (1983) found female *G. soricina* to be significantly larger than males in six of 14 external measurements (tail length, length of forearm, length of digit four, length of digit five, tibia length, and weight). Females were significantly larger than males in three of 16 cranial measurements

(greatest length of skull, mastoid breadth, and length of mandibular toothrow), whereas males were significantly larger than females in two other cranial measurements (width across molars and length of coronoid process). J. A. Allen (1911) and Tamsitt and Valdivieso (1963) noted that females of *G. longirostris* averaged larger than males, but that the sexes were not noticeably different in size in *G. soricina*. It appears that, in general, females average larger than males in antero-posterior measurements of the cranium, whereas males generally average larger than females in measurements of cranial width. Because of this size discrepancy, the sexes have been treated separately in analyses of individual and geographic variation.

Secondary sexual dimorphism in size is known in other glossophagines. Females were found to be significantly larger than males for some measurements in *Choeroniscus intermedius* (Genoways *et al.*, 1973), and averaged larger than males in *C. godmani* (LaVal, 1969; Gardner *et al.*, 1970) and *Hylonycteris underwoodi* (Phillips and Jones, 1971). However, males were found to be significantly larger than females for some measurements in *Anoura cultrata* (Nagorsen and Tamsitt, 1981), *A. caudifer* (Taddei, 1975), and in the related *Brachyphylla cavernarum* (Swanepoel and Genoways, 1978).

Individual Variation

External and cranial measurements.—Individual variation was assessed for each sex in five species of *Glossophaga*. The coefficients of variation (CV) for most measurements were less than 3.5 (Table 1) and are comparable to CV values found in other glossophagines (*Choeroniscus intermedius*—Genoways *et al.*, 1973; *Leptonycteris nivalis*—Martínez and Villa-R., 1940; *Anoura caudifer* and *Glossophaga soricina*—Taddei, 1975) and in the flower bats, *Erophylla bombifrons* and *E. sezekorni* (Buden, 1976). Wing measurements were more variable on the average than those of the cranium, and males were more variable than females in most parameters. Interorbital breadth and depth of braincase were the most variable cranial characters examined, a reflection, in part, of the difficulty in precisely obtaining these measurements. Greatest length of skull, condylobasal length, mastoid breadth, and mandibular length had the least amount of variation associated with any measurement.

External and cranial morphology.—Little variation in external and cranial morphology was found in *Glossophaga*. An adult male (MSB 26787) of *G. commissarisi* from Costa Rica had no joint between the metacarpal and phalanx in the fourth digit, the bones being completely fused. A small medial invagination on the posterior border of the palate was present in an adult male (LACM 14128) of *G. commissarisi* from Chiapas.

Hyperdontia.—Extra teeth were found in seven of 296 specimens (2.4 percent) of *G. commissarisi*. Two (TCWC 31238 and USNM 315254) individuals had an extra lower incisor on the right side. Five other specimens had an extra upper premolar

between C1 and P3; one (USNM 362463) on the right side, three (KU 102367, USNM 334164 and 335171) on the left side, and one (USNM 362468) on both sides. The incidence of extra incisors and premolars was not significantly different between the sexes in *G. commissarisi*.

Extra teeth were found in two of 131 specimens (1.5 percent) of *G. leachii*—an adult female (TCWC 17104) from Honduras had an extra upper premolar between the left canine and first premolar and an adult female (TCWC 21494) from El Salvador had an extra molariform tooth caudad to the third upper molar on both sides.

Four of 194 specimens (2.1 percent) of *G. longirostris* exhibited hyperdontia. An adult female (AMNH 179960) from Trinidad had an extra upper incisor, and three other females (AMNH 176607, MVZ 113899, and USNM 388949) each had an extra lower incisor. The incidence of supernumary lower incisors was not significantly different between the sexes in *G. longirostris*. Hyperdontia was not found in 68 specimens examined of *G. morenoi*.

Supernumary teeth were found in 11 of 841 individuals (1.3 percent) of *G. soricina*. An adult female (USNM 512270) possessed an extra lower incisor between the left outer incisor and canine. An extra premolar between the upper canine and first premolar was found in six specimens as follows: one (MVZ 135515) on the right side; four (AMNH 96091 and 126775, LSU 14113, and USNM 332710) on the left side; and in one (AMNH 42623) on both sides, although the right tooth is missing the alveolus remains. One adult male (USNM 313737) had three upper premolars on the left side; the extra tooth, similar to P4 in shape, was between P4 and M1. An extra molariform tooth was found between P4 and M1 on both sides in an adult female (LSU 12092) from Perú, and an extra third lower molar was found on the left side in two (LSU 3609 and UMMZ 92928) other individuals. The incidence of extra premolars and molars was not significantly different between the sexes in *G. soricina*.

Phillips (1971) did not find hyperdontia in 101 specimens of *G. commissarisi* or 136 specimens of *G. leachii*, but 14 of 818 individuals (1.7 percent) of *G. soricina* (all deposited at KU and not discussed above) had at least one extra tooth. Supernumary teeth most frequently involved upper premolars (53.9 percent) and lower incisors (30.8 percent) in both studies, and the former may represent either a single-rooted atavistic P2 or result from the double initiation of P3 (Phillips, 1971). Hyperdontia has been reported in additional specimens of *G. commissarisi* and *G. soricina* from México that I have not examined (Ramírez-P. and Müdespacher, 1987).

Dental morphology.—Three specimens of *Glossophaga* evinced dental abnormalities. An adult male (AMNH 178659) of *G. longirostris* from Trinidad lacked the metacrista and metastyle on both second upper molars; the remainder of the dental arcade was normal. A juvenile female (MSU 11310) of *G. soricina* from Colima possessed an incompletely duplicated P4 on both sides, the posterior cusp

TABLE 2.—*Timing of molt in five species of Glossophaga. Adult specimens examined were selected at random from throughout the range of five species. The total number of specimens examined is followed by the number of individuals in the process of molt (with the percent of total individuals in parentheses below).*

Month	<i>G. commissarisi</i>	<i>G. leachii</i>	<i>G. longirostris</i>	<i>G. morenoi</i>	<i>G. soricina</i>
January	36–0	0–0	18–0	4–0	82–3 (3.7)
February	50–2 (4.0)	9–3 (33.3)	4–0	5–4 (80.0)	149–20 (13.4)
March	24–3 (12.5)	5–0	12–0	9–0	135–9 (6.7)
April	13–1 (7.7)	16–3 (18.8)	2–0	6–0	95–5 (5.3)
May	7–1 (14.3)	6–0	1–0	2–0	76–9 (11.8)
June	7–0	23–0	26–4 (15.4)	5–0	98–13 (13.3)
July	35–3 (8.6)	34–0	15–2 (13.3)	17–0	206–8 (3.9)
August	42–5 (1.2)	20–1 (5.0)	23–4 (17.4)	6–0	119–17 (14.3)
September	6–1 (16.7)	4–0	5–1 (20.0)	1–0	34–3 (8.8)
October	9–0	7–0	9–1 (11.1)	1–0	72–6 (8.3)
November	13–0	6–0	9–3 (33.3)	10–0	59–0
December	7–0	0–0	20–0	2–0	38–2 (5.3)

being less developed than the anterior. An incompletely duplicated P3 on the left side was found in an adult male (FMNH 72184) of *G. soricina* from Colombia; both cusps were equally developed in this tooth.

Variation in pelage.—Albinism is a rare condition in *Glossophaga*, having been reported only in one specimen of *G. longirostris* (Setzer, 1950) and two individuals of *G. soricina* (Goodwin and Greenhall, 1964; Schneider, 1925). These individuals and another of *G. soricina* collected by A. L. Gardner (personal communication) had red irises and white fur and membranes. In addition, a specimen of *G. soricina* from Colombia was partially albinistic with gray membranes and fur, the individual hairs having dark bases and white tips. Occasional individuals of *G. commissarisi*, *G. longirostris*, and *G. soricina* had small randomly placed patches of white fur interspersed throughout otherwise normally-colored pelage, but there was no sexual or geographic pattern to this variation.

The sequence of molt has been described in specimens of *G. soricina* from the Yucatán Peninsula (Jones *et al.*, 1973) and *G. longirostris* from northern South America (Webster and Handley, 1986). Molt begins as an overall growth of new hair beneath the old in both species, the old hair being replaced in asymmetrical patches as the new hair grows to about half its normal length. Hair on the head and shoulders is generally lost first, but in some specimens the pelage on the back is replaced initially.

The timing of molt (Table 2) appears to be broadly asynchronous in five species of *Glossophaga* in that specimens from any one locality exhibit all stages of pelage replacement (from possessing only old worn hair to only new unworn hair) at any one time. *Glossophaga commissarisi* was found molting in all months from February to September except June, and specimens of *G. longirostris* were found in the process of molt from June to November (Webster and Handley, 1986). Specimens from throughout the range of *G. soricina* were molting in all months except November, but local patterns of molt were not apparent. Molt does not appear to be restricted to reproductively inactive females in that individuals of *G. commissarisi* (USNM 309377), *G. longirostris* (KU 118110), and *G. soricina* (AMNH 147938, MSU 11309, and USNM 508515) were either pregnant or lactating while in the process of molt.

SYSTEMATIC ACCOUNTS

Genus *Glossophaga*

1818. *Glossophaga* É. Geoffroy St.-Hilaire, Mém. Mus. Hist. Nat., Paris, 4:418; type, *Vespertilio soricinus* Pallas.
1838. *Phyllophora* Gray, Mag. Zool. Bot., 2:489; type, *Phyllophora amplexicaudata* Gray (= *Glossophaga amplexicaudata* Spix).
1847. *Nicon* Gray, Proc. Zool. Soc. London, p. 15, 13 April; type, *N[icon]. caudifer* Gray (= *Monophyllus leachii* Gray).

Diagnosis

Rostrum slightly elongate, but shorter than braincase; tongue extremely protrusible, covered with numerous papillae anteriorly and labially; dental formula, i 2/2, c 1/1, p 2/3, m 3/3, total 34; inner upper incisor with broad oblique cutting edge, tapering to a narrow base; outer upper incisor with pointed crown and reduced cutting edge; lower incisors variable in size but always well developed; premolars not reduced and lacking conspicuous styles, the individual teeth in contact or with only small gaps between them; upper molars in contact, with protocone and mesostyle reduced, hypocone absent; first and second molars subequal in size and with posterolabially directed metastyles, the third smaller and lacking metacrista and metastyle; lower molars in contact, trigonid well developed, hypoconid reduced; zygoma complete; braincase large, rounded, smooth;

pterygoid hamulae unmodified, not inflated; tympanic ring covering less than half of cochlear surface; tail shorter than tibia, the tip barely extending from middle of unreduced interfemoral membrane.

Comparisons

Bats of the genus *Glossophaga* can be separated from other known glossophagines by dental formula (*Anoura*, *Brachyphylla*, *Choeroniscus*, *Choeronycteris*, *Erophylla*, *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, *Musonycteris*, *Phyllonycteris*, and *Scleronycteris*), complete zygoma (*Lionycteris* and *Lonchophylla*), and/or relatively primitive teeth (*Monophyllus* and *Platalina*). The inner upper incisors are not spatulate and the robust premolars and molars are usually in contact in *Glossophaga*, whereas in some glossophagines the postcanine teeth have distinct gaps between them.

Monophyllus (endemic to the Greater and Lesser Antilles) most closely resembles *Glossophaga* but is larger in most external and cranial dimensions, particularly the length of the tibia. In addition, the former has much smaller upper and lower incisors with distinct gaps between the teeth, the premolars have conspicuous cingular styles, the interfemoral membrane is greatly reduced, the tail extends well beyond the uropatagium, and M1 and M2 appear squared in occlusal outline due to an expanded hypoconal basin. In *Glossophaga*, the upper incisors are large and usually in contact, the premolars possess small stylets, the interfemoral membrane extends to the knees, the tail is enclosed in the uropatagium, and M1 and M2 taper posterolabially because a hypocone is absent. The genera presently are known to be sympatric only on Jamaica (*M. r. redmani* and *G. soricina antillarum*) and St. Vincent (*M. plethodon luciae* and *G. longirostris rostrata*).

Key to the Species of *Glossophaga* (modified from Webster and Jones, 1984b)

1. Lower incisors large, usually in contact, forming a complete arc between canines; upper incisors greatly procumbent 2
2. Inner upper incisor larger than outer in bulk (occlusal view); pterygoid alae present; mandibular symphyseal ridge prominent; parastyle of M1 well developed *G. soricina*, p. 104
- 2'. Inner upper incisor subequal to outer in bulk (occlusal view); pterygoid alae absent or poorly developed; mandibular symphyseal ridge reduced; parastyle of M1 reduced *G. longirostris*, p. 68
- 1'. Lower incisors reduced in size, separated by distinct gaps; upper incisors noticeably procumbent only in *G. morenoi* 3
3. Upper incisors procumbent, inner pair larger than outer in bulk (occlusal view); anterior border of premaxillae elongate *G. morenoi*, p. 96
- 3'. Upper incisors not procumbent, inner pair subequal to, or smaller than, outer in bulk (occlusal view); anterior border of premaxillae evenly rounded between canines . . . 4

- 4. Lower incisors small, peglike; presphenoid ridge flattened subterminally; pterygoid alae usually absent *G. commissarisi*, p. 23
- 4'. Lower incisors moderately large; presphenoid ridge complete; pterygoid alae usually present *G. leachii*, p. 50

Because the five sibling species of *Glossophaga* exhibit some variation in the key characters used above, identification is sometimes difficult. In areas of sympatry, however, character displacement is noticeable (particularly in southern México and Central America) and the species can be distinguished easily in the field by examining the morphology of the upper and lower incisors with a hand lens. I collected four (*G. commissarisi*, *G. leachii*, *G. morenoi*, and *G. soricina*) of the five species of *Glossophaga* from the same mist net in western Chiapas (on the Río Ocuilapa near Tonalá) and had little difficulty separating them. *G. commissarisi* was noticeably smaller in size and darker in color than the other species; the upper incisors were not noticeably procumbent; the lower incisors were markedly reduced in size; and the rostrum was relatively short. Specimens of *G. leachii* resembled *G. commissarisi* with short rostra, reduced lower incisors, and upper incisors that were not noticeably procumbent, but individuals of *G. leachii* averaged larger than *G. commissarisi* in body size and were paler in color. *G. morenoi* was distinguished easily from the other species by its extremely elongate rostrum, procumbent upper incisors, reduced lower incisors, and more distinctly bicolored dorsal pelage (the bases of the individual hairs tend to be more cream-colored rather than brownish). *G. soricina* was characterized by a moderately elongate rostrum, noticeably procumbent upper incisors, and large lower incisors. More detailed comparisons can be found in the following species accounts.

Glossophaga commissarisi
Commissaris' Long-tongued Bat

This bat has a disjunct distribution. One race occurs in western México from central Sinaloa and southwestern Durango southward to Colima; another race occurs from southern México (central Veracruz and eastern Oaxaca, excluding the Yucatán Peninsula) southeastward to eastern Panamá and probably occurs in western Colombia as well; and the third race is known from the upper Amazon Basin of southern Colombia, eastern Ecuador and Perú, and western Brazil.

Diagnosis

Smallest member of the genus in most measurements, particularly those of the wing, rostrum, and tooththrows; upper incisors not noticeably procumbent, I2 equal to, or larger than, I1 in bulk; fourth upper premolar with conspicuous posterolingual cingular shelf; parastyle of first upper molar directed labially to posterolabially from paracone; lower incisors small, subcircular in occlusal view, with distinct

gaps between teeth, the inner pair usually smaller than the outer in bulk; premaxillae evenly rounded between canines and not noticeably elongate; pterygoid alae absent; presphenoid ridge flattened subterminally; postpalatal processes poorly developed; mandibular symphyseal ridge well developed; averaging darker in pelage coloration in southern México and Central America than other species of *Glossophaga*, Cinnamon Brown to Fuscous dorsally, Avellaneous to Clove Brown ventrally; weight averaging 8.8 (6.8-12) in males and 9.0 (6.7-12) in nonparous females from throughout the range.

Comparisons

Glossophaga commissarisi can be distinguished from *G. leachii* in that it usually lacks pterygoid alae, has a subterminally flattened presphenoid ridge, and has small lower incisors that are subcircular in occlusal view (subtriangular in *G. leachii*). Although there is some overlap in external and cranial measurements, *G. commissarisi* averages smaller than *G. leachii* in those of the wing and in body weight, and averages darker in color over most of the region in which they are sympatric.

Compared with *G. longirostris*, *G. commissarisi* is much smaller in most external and cranial measurements. In *G. commissarisi* the upper incisors are not noticeably procumbent; the fourth upper premolar has a distinct posterolingual cingular shelf; the parastyle of M1 is well developed; the lower incisors are reduced, subcircular in occlusal view, and have distinct gaps between the teeth; the presphenoid ridge is flattened subterminally; the basisphenoid pits are deep; the slope of the rostrum is more abrupt; and the mandibular symphyseal ridge is well developed. In *G. longirostris*, as compared with *G. commissarisi*, the upper incisors are noticeably procumbent; the fourth upper premolar frequently lacks the posterolingual cingular shelf; the parastyle of M1 is reduced; the lower incisors are large, subtriangular in occlusal view, and usually in contact; the presphenoid ridge is high and complete throughout; the basisphenoid pits are shallow; and the mandibular symphyseal ridge is poorly developed. Also, these species are not sympatric as presently understood.

Glossophaga commissarisi can be distinguished from *G. morenoi* by its small size (particularly in measurements reflecting cranial length), less procumbent upper incisors, well-developed parastyle of the first upper molar that is directed labially to posterolabially (poorly developed and directed anterolabially in *G. morenoi*), deeper basisphenoid pits, more abrupt slope of rostrum, and poorly developed postpalatal processes. *G. commissarisi* averages darker than *G. morenoi*, particularly where the two species are sympatric in southern México.

Specimens of G. commissarisi can be distinguished from those of *G. soricina* in that the upper incisors are subequal in bulk, or if unequal the outer pair the larger, and not noticeably procumbent (inner pair the larger and incisors procumbent in *G. soricina*), the parastyle of M1 is directed labially to posterolabially (anterolabially

in *G. soricina*), and the lower incisors are reduced with noticeable gaps between the teeth (large and in contact in *G. soricina*). In addition, *G. commissarisi* lacks pterygoid alae and a well-developed presphenoid ridge, whereas *G. soricina* possesses both of these characters; the basisphenoid pits are usually deep in *G. commissarisi* and shallow in *G. soricina*; and the postpalatal processes are usually poorly developed in *G. commissarisi* but well developed in *G. soricina*. Where these species are sympatric in southern México and Central America, *G. commissarisi* averages smaller in most measurements and darker in pelage color; however, *G. commissarisi* and *G. soricina* are similar in size and coloration in western México and the upper Amazon Basin where they are also sympatric.

Ecology

Glossophaga commissarisi occupies a wide variety of subtropical and tropical habitats including savanna, xeric thorn forest, pine-oak forest, and deciduous and evergreen rainforests. Most individuals have been collected in mist nets set across streams and trails in forests or around fruit groves, but these bats also have been taken in villages, probably owing to the proximity of suitable food. Known daytime roosts include caves, culverts, and hollows of living trees. Ecological observations can be found in Albuja (1983), Baker and Greer (1962), Gardner (1962), Handley (1966), Helleybuyck *et al.* (1985), Jones (1964), Jones *et al.* (1972), Medellín (1988), Watkins *et al.* (1972), and Webster and Jones (1982, 1983, 1987).

Howell and Burch (1974) examined the stomach contents of seven individuals of *G. commissarisi* collected in Costa Rica in May. Three specimens had eaten lepidopterans, two had consumed fruit (Solanaceae: *Acnistus*), one had eaten legume nectar and pollen (Papilionoideae: *Macuna*), and one had eaten banana nectar and pollen (Musaceae: *Musa*). Apparently, this species, like its congeners, is rather catholic in diet and opportunistically consumes pollen, nectar, soft fruits, and soft-bodied insects.

The time of capture, recorded from the specimen labels of 26 individuals, indicates that *G. commissarisi* is most frequently collected before 9:00 PM (57.7 percent) or from 9:00 to midnight (23.1 percent). Decreased activity apparently occurs between midnight to 3:00 AM (11.5 percent) and 3:00 to 6:00 AM (7.7 percent).

LaVal (1970) banded 21 *G. commissarisi* in Costa Rica, but these bats were not recaptured in five subsequent nights of mist netting. Trombiculid mites (*Hooperella saccopteryx*, *H. vesperuginis*, and *Speleocola secunda*) are known to parasitize this species (Webb and Loomis, 1977).

Geographic Variation

Univariate Analyses

Adult specimens from throughout the geographic range of *G. commissarisi* were grouped into 10 samples (see Fig. 1) as follows: *sample 1*—SINALOA, DURANGO, and NAYARIT; *sample 2*—JALISCO and COLIMA; *sample 3*—VERACRUZ, OAXACA, and CHIAPAS (San Clemente, Tonalá, and Cintalapa); *sample 4*—CHIAPAS (Margaritas, Solusuchiapa, Sabana de San Quintín, Escuintla, Hueheután, Cacahuatán, Pijijiapan, Huixtla, and Tapachula), GUATAMALA (Alta Verapaz and Petén), and BELIZE; *sample 5*—GUATAMALA (Jutiapa, San Marcos, Santa Rosa, and Sololá); *sample 6*—EL SALVADOR and HONDURAS; *sample 7*—NICARAGUA; *sample 8*—COSTA RICA and PANAMA (Bocas del Toro and Chiriquí); *sample 9*—PANAMA (Coclé, Colón, Panamá, San Blas, and Darién); *sample 10*—COLOMBIA (Amazonas). Standard statistics for all geographic samples are given in Table 3, and the results of four (length of fifth metacarpal, greatest length of skull, interorbital breadth, and width across molars) SS-STP tests are given in Table 4.

External measurements.—Specimens from western México (samples 1-2) and those from southern Colombia (sample 10) average much larger than specimens from Middle America in measurements of the wing (Table 3). Bats from Veracruz, Oaxaca, and western Chiapas (sample 3) are moderately large, whereas those from Chiapas, northern Guatemala, Belize, El Salvador, and Honduras (samples 4-6) have wing measurements that average in the middle of the range for the species. Specimens from Nicaragua, Costa Rica, and Panamá (7-9) tend to be smaller than average.

Cranial measurements.—Specimens from western México (samples 1-2) and southern Colombia (10) average larger than those from all other samples in greatest length of skull and condylobasal length, whereas individuals from Chiapas, Belize, and Guatemala (4-5), particularly the females, tend to be smaller than average for the species. Specimens from sample 6 (El Salvador and Honduras) are moderately large, and individuals from Veracruz, Oaxaca, western Chiapas, Nicaragua, Costa Rica, and Panamá (3,7-9) average in the middle of the range for the species in greatest length of skull and condylobasal length.

Patterns of variation in length of rostrum and length of maxillary and mandibular toothrows are similar. Specimens from western México, El Salvador, and Honduras (1-2, 6) average larger than those in other samples, whereas populations from Chiapas, Belize, and Guatemala (4-5), particularly the females, average smaller. All other samples (3, 7-10) average in the middle of the range for the species. The two males from southern Colombia (10) have toothrows that are larger than average relative to other males, but the female from the same locality has a relatively shorter rostrum and shorter toothrows than other females.

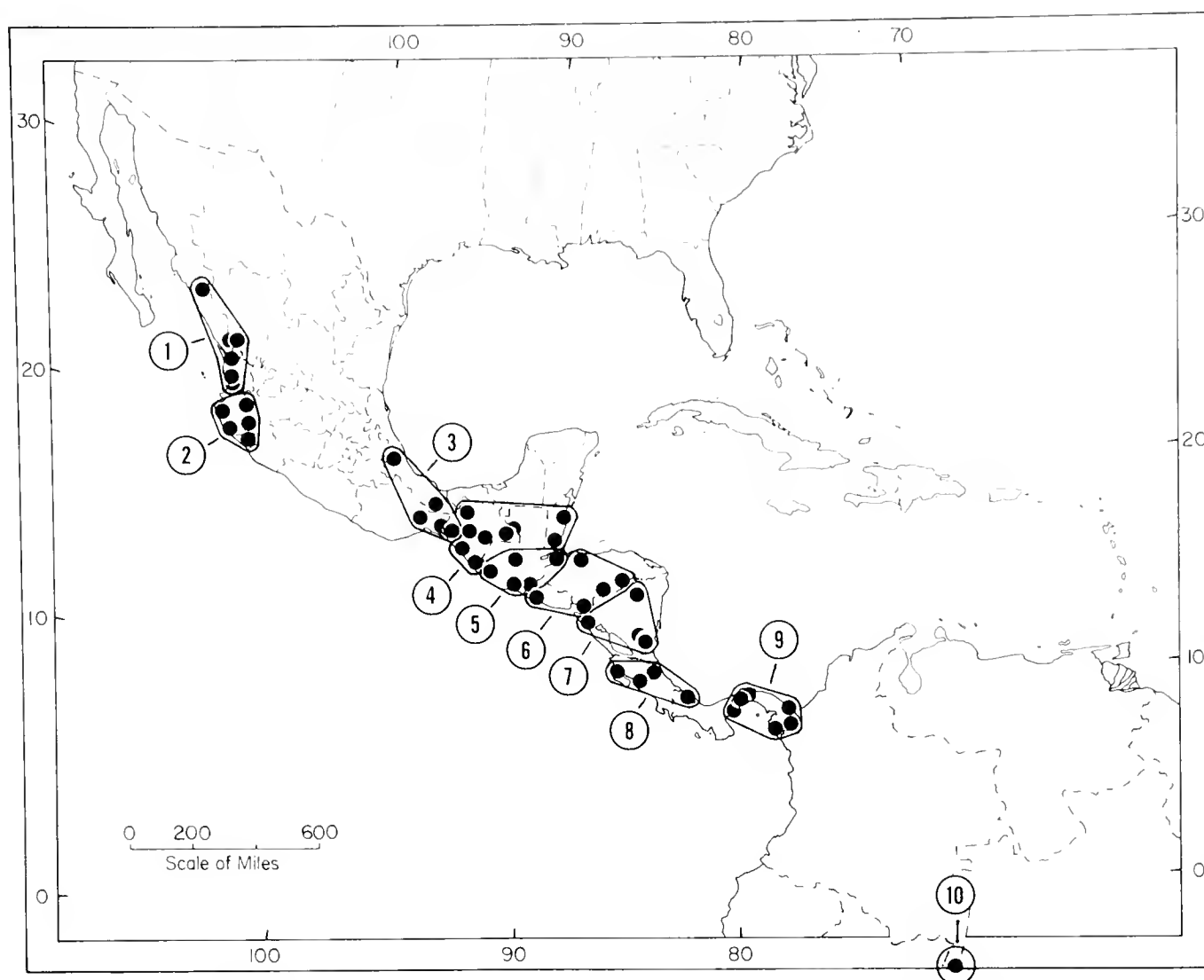


FIG. 1.—Approximate geographic areas included in the 10 samples of *Glossophaga commissarisi* analyzed. See text for localities included in each sample.

Geographic variation in mandibular length is similar to that described in the preceding paragraph except that specimens from eastern Panamá (9) are larger than average, and individuals from Sinaloa, Durango, and Nayarit (1) average in the middle of the range for the species.

Measurements reflecting cranial width (zygomatic breadth, mastoid breadth, interorbital breadth, breadth of braincase, and width across molars) follow similar geographic trends. Bats from samples 1-2 (western México) and males from southern Colombia (10) average larger than those in all other samples, and specimens from Chiapas, Belize, northern Guatamala, Costa Rica, and western Panamá, and the female from southern Colombia (4, 8, 10) are smaller than average. Specimens from Veracruz, Oaxaca, western Chiapas, southern Guatamala, El Salvador, Honduras, Nicaragua, and eastern Panamá (3, 5, 7-9) tend to average in the middle of the range for the species.

The pattern of geographic variation in depth of braincase appears unique in *G. commissarisi*. Specimens from samples 4 and 10 (Chiapas, Belize, northern Guatamala, and southern Colombia) are intermediate between large individuals from samples 1-3 (Sinaloa, Durango, Nayarit, Jalisco, Colima, Veracruz, Oaxaca,

TABLE 3.—*Geographic variation in external and cranial measurements among 10 samples of Glossophaga commissarisi. See text and Figure 1 for key to sample numbers.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of forearm</i>								
1	7	34.40	32.7–35.6	1.83	12	34.98	33.9–36.6	1.82
2	5	34.36	33.2–35.6	1.94	16	35.01	33.2–36.2	1.85
3	31	33.91	31.1–36.2	2.39	34	34.56	32.0–37.4	2.74
4	13	33.43	32.3–35.8	1.83	15	34.06	32.1–35.9	2.19
5	9	33.16	32.3–34.5	1.45	10	33.21	32.6–34.8	1.28
6	11	33.10	32.1–34.0	1.25	14	34.34	32.7–36.8	2.39
7	10	33.35	31.9–34.2	1.40	9	33.89	32.5–34.9	1.49
8	26	32.69	31.3–35.3	2.06	24	33.72	32.1–35.3	1.79
9	21	32.89	31.6–34.0	1.35	19	33.54	32.0–35.1	1.55
10	2	34.95	34.0–35.9	2.69	1	35.20		
<i>Length of third metacarpal</i>								
1	7	34.41	33.4–35.7	1.75	12	34.57	33.1–37.3	2.42
2	5	34.16	32.6–35.7	2.49	16	34.88	33.0–36.0	1.77
3	33	33.69	31.7–35.4	2.15	34	34.10	31.6–36.4	2.37
4	13	33.56	32.7–35.9	1.71	15	33.90	32.4–35.8	1.78
5	9	33.02	32.2–34.2	1.21	10	33.03	31.1–35.7	2.35
6	11	33.35	32.3–34.2	1.05	14	34.18	32.4–35.7	2.18
7	10	32.91	31.7–34.3	1.67	9	33.68	32.3–34.6	1.97
8	26	32.57	30.8–35.6	2.41	24	33.50	31.6–35.6	1.86
9	21	32.61	31.1–34.2	1.35	19	33.29	30.8–35.2	2.02
10	2	34.60	34.3–34.9	0.85	1	36.20		
<i>Length of fourth metacarpal</i>								
1	7	31.79	30.7–32.6	1.33	12	31.73	30.5–34.0	2.06
2	5	31.68	30.1–32.9	2.21	16	32.43	30.8–33.9	1.86
3	33	31.61	29.7–33.5	1.86	34	31.96	29.5–33.8	1.96
4	13	31.11	30.2–33.6	1.79	15	31.52	30.5–33.3	1.82
5	9	30.67	29.2–31.8	1.48	10	30.90	29.4–33.4	2.17
6	11	30.88	29.8–31.5	1.07	14	31.77	29.6–33.3	2.13
7	10	30.52	29.4–31.5	1.33	9	31.16	29.6–32.0	1.67
8	26	30.10	28.3–33.0	2.36	24	31.17	29.7–33.4	1.83
9	21	30.37	28.5–31.5	1.51	19	30.72	29.9–32.4	1.52
10	2	32.50	32.0–33.0	1.41	1	34.40		
<i>Length of fifth metacarpal</i>								
1	7	31.66	30.4–32.9	1.74	12	31.97	30.8–34.0	1.93
2	5	31.58	30.6–32.7	1.97	16	32.18	30.3–33.9	1.96
3	33	31.21	28.8–33.4	2.22	34	31.55	28.5–34.1	2.42
4	13	30.61	29.6–32.8	1.64	15	30.97	29.3–32.4	1.67
5	9	30.27	29.1–31.7	1.66	10	30.12	28.3–33.6	3.01
6	11	30.47	29.5–31.3	1.07	14	31.40	29.6–33.6	2.27
7	10	30.06	28.5–31.5	1.73	9	30.73	29.9–31.9	1.42
8	26	29.52	27.8–32.3	2.13	24	30.60	28.8–32.7	2.04
9	21	29.80	28.7–30.9	1.32	19	30.28	29.2–31.8	1.48
10	2	32.10	31.7–32.5	1.13	1	33.80		

TABLE 3.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Greatest length of skull</i>								
1	7	20.53	20.3–20.8	0.40	13	20.65	20.0–21.3	0.68
2	5	20.70	20.3–21.1	0.68	16	20.69	20.2–21.2	0.52
3	31	20.18	19.3–21.0	1.04	32	20.27	19.5–21.3	1.01
4	13	20.04	19.4–20.6	0.69	15	19.93	19.3–20.8	0.81
5	9	20.01	19.6–20.6	0.64	10	19.85	19.5–20.4	0.61
6	11	20.26	19.6–20.6	0.71	13	20.54	20.1–21.1	0.64
7	10	20.17	19.7–20.6	0.67	9	20.49	19.7–20.8	0.66
8	24	20.00	19.1–21.0	0.84	24	20.23	19.7–21.1	0.78
9	21	20.24	19.9–20.8	0.49	19	20.29	19.9–20.8	0.46
10	2	20.45	20.1–20.8	0.99	1	20.40		
<i>Condylobasal length</i>								
1	7	18.69	18.6–18.9	0.24	13	18.85	18.4–19.3	0.59
2	5	18.80	18.5–19.1	0.49	16	18.83	18.3–19.3	0.58
3	32	18.48	17.2–19.3	1.05	32	18.63	17.8–19.6	0.99
4	13	18.35	17.9–19.1	0.59	15	18.25	17.5–19.0	0.80
5	9	18.42	18.2–18.9	0.55	10	18.33	18.0–18.7	0.50
6	11	18.54	18.0–18.9	0.69	14	18.82	18.5–19.4	0.63
7	10	18.44	18.0–18.8	0.54	9	18.77	18.0–19.2	0.81
8	24	18.33	17.5–19.2	0.86	23	18.60	17.9–19.4	0.81
9	21	18.56	17.9–19.1	0.58	18	18.56	18.2–19.0	0.50
10	2	18.85	18.5–19.2	0.99	1	18.90		
<i>Zygomatic breadth</i>								
1	7	9.60	9.4–9.9	0.33	11	9.38	8.9–9.8	0.50
2	5	9.70	9.6–9.9	0.25	16	9.50	9.3–9.7	0.23
3	32	9.51	9.0–10.1	0.58	29	9.46	9.1–10.3	0.58
4	10	9.41	9.0–10.0	0.63	12	9.32	8.9–9.6	0.47
5	8	9.45	9.1–9.8	0.40	9	9.26	9.1–9.5	0.35
6	11	9.61	9.0–10.0	0.56	14	9.53	9.1–9.9	0.45
7	10	9.41	9.0–9.7	0.42	9	9.46	9.0–9.8	0.51
8	26	9.25	8.6–9.8	0.68	24	9.39	8.8–10.0	0.61
9	21	9.37	8.9–9.8	0.50	17	9.40	9.0–9.7	0.44
10	1	9.30			1	9.30		
<i>Length of rostrum</i>								
1	7	7.99	7.8–8.1	0.24	14	8.02	7.8–8.3	0.34
2	5	8.06	7.7–8.3	0.46	16	8.10	7.9–8.4	0.28
3	34	7.84	7.3–8.3	0.49	34	7.98	7.5–8.5	0.49
4	13	7.85	7.6–8.2	0.35	15	7.79	7.4–8.1	0.50
5	9	7.87	7.7–8.2	0.35	10	7.86	7.7–8.0	0.21
6	11	7.90	7.6–8.1	0.33	14	8.01	7.7–8.3	0.38
7	10	7.84	7.5–8.1	0.38	9	8.06	7.6–8.4	0.49
8	25	7.82	7.4–8.2	0.43	24	7.99	7.6–8.3	0.40
9	21	7.91	7.6–8.3	0.33	19	7.98	7.7–8.2	0.30
10	2	7.85	7.8–7.9	0.14	1	7.90		

TABLE 3.—*Continued.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Mastoid breadth</i>								
1	7	9.13	9.0–9.4	0.30	14	9.14	8.7–9.5	0.34
2	5	9.18	9.0–9.3	0.22	16	9.14	8.8–9.4	0.32
3	33	9.05	8.6–9.5	0.52	33	9.05	8.8–9.6	0.42
4	13	8.93	8.4–9.5	0.58	15	8.87	8.5–9.2	0.38
5	9	9.00	8.7–9.4	0.42	10	8.80	8.6–9.0	0.25
6	11	9.10	8.9–9.3	0.28	14	8.98	8.7–9.3	0.33
7	10	8.98	8.7–9.2	0.31	9	8.98	8.7–9.3	0.42
8	26	8.85	8.5–9.3	0.44	24	8.95	8.5–9.5	0.46
9	21	9.06	8.6–9.4	0.45	19	8.97	8.7–9.4	0.36
10	2	9.00	9.0	0.00	1	8.70		
<i>Interorbital breadth</i>								
1	7	4.30	4.2–4.4	0.16	14	4.21	4.0–4.4	0.23
2	5	4.36	4.3–4.4	0.11	16	4.28	3.9–4.4	0.25
3	34	4.06	3.7–4.4	0.30	34	4.04	3.8–4.3	0.28
4	13	3.99	3.7–4.2	0.28	15	3.99	3.8–4.3	0.26
5	9	4.13	3.9–4.4	0.32	10	4.05	3.9–4.2	0.24
6	11	4.08	3.9–4.2	0.22	14	4.09	3.8–4.2	0.26
7	10	4.09	3.9–4.4	0.35	9	4.11	3.8–4.4	0.34
8	26	3.99	3.8–4.2	0.29	25	4.08	3.8–4.3	0.32
9	21	4.11	3.9–4.3	0.25	13	4.08	3.9–4.3	0.27
10	2	4.05	4.0–4.1	0.14	1	4.00		
<i>Breadth of braincase</i>								
1	7	8.50	8.4–8.8	0.28	14	8.45	8.1–8.6	0.29
2	5	8.52	8.4–8.6	0.17	16	8.52	8.3–8.9	0.28
3	34	8.46	8.2–8.9	0.30	33	8.48	8.3–8.8	0.27
4	13	8.43	8.0–8.8	0.46	15	8.46	8.2–8.9	0.35
5	9	8.44	8.2–8.7	0.33	10	8.37	8.1–8.6	0.33
6	11	8.57	8.3–8.9	0.36	14	8.44	8.0–8.7	0.34
7	10	8.42	8.2–8.7	0.34	9	8.43	8.1–8.8	0.47
8	26	8.31	8.0–8.7	0.38	24	8.37	8.0–8.7	0.34
9	21	8.38	8.0–8.7	0.38	19	8.36	8.1–8.6	0.33
10	2	8.65	8.4–8.9	0.71	1	8.30		
<i>Depth of braincase</i>								
1	7	7.00	6.9–7.1	0.12	13	6.94	6.6–7.2	0.37
2	5	7.06	7.0–7.3	0.27	16	6.99	6.7–7.3	0.31
3	32	6.97	6.6–7.2	0.31	33	6.94	6.6–7.3	0.32
4	13	6.90	6.6–7.3	0.41	15	6.89	6.6–7.2	0.32
5	9	7.06	6.9–7.3	0.28	10	6.83	6.6–7.3	0.43
6	11	7.05	6.8–7.4	0.43	14	6.84	6.5–7.2	0.47
7	10	6.83	6.4–7.2	0.51	9	6.74	6.5–7.1	0.33
8	25	6.75	6.3–7.1	0.44	24	6.77	6.4–7.3	0.40
9	21	6.76	6.0–7.3	0.56	18	6.71	6.3–7.2	0.45
10	2	6.90	6.7–7.1	0.57	1	6.90		

TABLE 3.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of maxillary tooththrow</i>								
1	7	6.87	6.5–7.1	0.40	14	6.96	6.7–7.3	0.35
2	5	6.92	6.6–7.2	0.43	16	6.99	6.7–7.3	0.30
3	32	6.88	6.5–7.3	0.44	34	6.91	6.5–7.4	0.47
4	13	6.82	6.5–7.0	0.33	15	6.81	6.5–7.1	0.39
5	9	6.78	6.6–7.0	0.28	10	6.80	6.6–7.1	0.33
6	12	6.99	6.7–7.7	0.56	13	6.98	6.6–7.3	0.46
7	10	6.78	6.5–7.0	0.37	9	6.96	6.6–7.3	0.41
8	26	6.72	6.3–7.0	0.38	25	6.95	6.6–7.2	0.35
9	21	6.86	6.6–7.1	0.30	19	6.93	6.7–7.1	0.20
10	2	6.95	6.8–7.1	0.42	1	6.90		
<i>Length of mandibular tooththrow</i>								
1	7	7.30	7.0–7.5	0.37	14	7.41	7.2–7.6	0.26
2	5	7.36	7.1–7.5	0.30	16	7.43	7.2–7.7	0.26
3	32	7.29	7.0–7.7	0.40	34	7.31	6.8–7.9	0.54
4	13	7.22	6.9–7.5	0.34	15	7.22	6.9–7.6	0.43
5	9	7.18	7.0–7.4	0.24	10	7.23	7.0–7.4	0.23
6	12	7.33	7.0–7.6	0.41	14	7.36	7.0–7.7	0.43
7	10	7.24	6.9–7.5	0.40	9	7.37	7.1–7.6	0.32
8	26	7.18	6.8–7.5	0.40	25	7.35	7.0–7.6	0.35
9	21	7.26	7.0–7.6	0.33	18	7.35	7.1–7.7	0.28
10	2	7.35	7.2–7.5	0.42	1	7.30		
<i>Width across molars</i>								
1	7	5.66	5.6–5.8	0.16	14	5.64	5.4–5.8	0.22
2	5	5.68	5.4–5.9	0.38	16	5.69	5.5–5.8	0.18
3	32	5.52	5.1–5.8	0.36	34	5.51	5.2–6.0	0.36
4	13	5.46	5.1–5.8	0.37	14	5.46	5.2–5.7	0.31
5	9	5.43	5.3–5.6	0.24	10	5.42	5.3–5.7	0.23
6	10	5.58	5.3–5.9	0.40	12	5.58	5.3–5.9	0.32
7	10	5.46	5.1–5.7	0.40	9	5.57	5.3–5.7	0.28
8	26	5.42	4.8–5.8	0.36	25	5.54	5.3–5.9	0.35
9	21	5.50	5.2–5.7	0.29	19	5.57	5.3–6.0	0.34
10	2	5.35	5.3–5.4	0.14	1	5.40		
<i>Mandibular length</i>								
1	7	12.91	12.8–13.1	0.27	14	13.01	12.7–13.3	0.37
2	5	13.04	12.6–13.4	0.64	16	13.08	12.6–13.6	0.53
3	34	12.88	12.4–13.6	0.65	33	13.06	12.6–13.8	0.74
4	13	12.73	12.3–13.4	0.58	15	12.83	12.3–13.5	0.76
5	9	12.73	12.6–12.9	0.26	10	12.65	12.4–13.0	0.41
6	12	12.93	12.5–13.3	0.58	14	13.17	12.8–13.6	0.47
7	10	12.86	12.4–13.3	0.47	9	13.08	12.3–13.5	0.75
8	26	12.73	12.0–13.4	0.79	25	13.00	12.4–13.5	0.56
9	21	12.97	12.7–13.3	0.43	17	13.14	12.8–13.5	0.41
10	2	12.90	12.7–13.1	0.57	1	13.10		

TABLE 4.—Results of four SS-STP tests of geographic variation in *Glossophaga commissarisi*. Vertical lines to the right of sample means connect maximally nonsignificant subsets at the 0.05 probability level for length of fifth metacarpal, greatest length of skull, interorbital breadth, and width across molars. See text and Figure 1 for key to sample numbers.

Sample number	Males		Sample number	Females	
	Mean	Results SS-STP		Mean	Results SS-STP
Length of fifth metacarpal					
10	32.10		10	33.80	
1	31.66		2	32.18	
2	31.58		1	31.97	
3	31.21		3	31.55	
4	30.61		6	31.40	
6	30.47		4	30.97	
5	30.27		7	30.73	
7	30.06		8	30.60	
9	29.80		9	30.28	
8	29.52		5	30.12	
Greatest length of skull					
2	20.69		2	20.70	
1	20.65		1	20.53	
6	20.54		10	20.45	
7	20.49		6	20.26	
10	20.40		9	20.24	
9	20.29		3	20.18	
3	20.27		7	20.17	
8	20.23		4	20.04	
4	19.93		5	20.01	
5	19.85		8	20.00	
Interorbital breadth					
2	4.28		2	4.36	
1	4.21		1	4.30	
7	4.11		5	4.13	
6	4.09		9	4.11	
8	4.08		7	4.09	
9	4.08		6	4.08	
5	4.05		3	4.06	
3	4.04		10	4.05	
10	4.00		4	3.99	
4	3.99		8	3.99	
Width across molars					
2	5.69		2	5.68	
1	5.64		1	5.66	
6	5.58		6	5.58	
9	5.57		3	5.52	
7	5.57		9	5.50	
8	5.54		4	5.46	
3	5.51		7	5.46	
4	5.46		5	5.43	
5	5.42		8	5.42	
10	5.40		10	5.35	

and western Chiapas) and small specimens from samples 7-9 (Nicaragua, Costa Rica, and Panamá). Males from Guatemala, El Salvador, Honduras (5-6) are larger relative to other males, but females from samples 5-6 average in the middle of the range for the species.

Pelage coloration.—Specimens from El Salvador, Honduras, and Nicaragua (6-7) average darker and those from Jalisco, Colima, Costa Rica, and Panamá (2, 8-9) average paler in pelage coloration than individuals from other samples (1, 3-5). Color was not determined for specimens from southern Colombia (10) because the skins are preserved in fluid.

Qualitative cranial characters (Table 5).—Pterygoid alae were absent in 88.4 percent of the specimens of *Glossophaga commissarisi* examined by me. They were modestly developed in 25 (8.5 percent) and well developed in only nine of 294 (3.1 percent) individuals examined. Specimens from western México (1-2), particularly those from Sinaloa, Durango, and Nayarit, have the highest incidence of moderate development of the pterygoid alae, whereas no individuals from El Salvador, Honduras, or southern Colombia (6, 10) possess these structures. Seven of nine specimens with well-developed pterygoid alae are from sample 3 (Veracruz, Oaxaca, and western Chiapas), and six of these are males.

The presphenoid ridge is flattened subterminally (87.8 percent) in *G. commissarisi*, especially in specimens from western México and Nicaragua (1-2, 7) where no bats exhibit a continuous presphenoid ridge. A continuous and prominent ridge is found only in specimens from southern México, northern Guatemala, Belize (3-4), but these eight individuals constitute only 2.7 percent of the 294 specimens examined. Twenty-eight (9.5 percent) individuals have moderately-procumbent presphenoid ridges, but these specimens are from southern México southward to Panamá (except Nicaragua) and southern Colombia (3-6, 8-10), and exhibit little geographic variation.

The angle of projection of the upper incisors in *G. commissarisi* is predominantly downward and not noticeably procumbent (89.5 percent), particularly in Nicaragua (7) where all individuals exhibit this character. Twenty-three of 286 (8.0 percent) specimens have moderately procumbent and seven (2.4 percent) have greatly procumbent upper incisors, the latter being from Colima, Veracruz, and Chiapas (2-4).

The upper incisors in *G. commissarisi* are equal (53.7 percent) or subequal (17.2 percent) in bulk. The high incidence of specimens with upper incisors that are unequal in bulk (29.1 percent) is attributable to those individuals in which the outer incisor is larger than the inner (rather than the opposite as is found in *G. soricina*); therefore, continuity in this multistate character is not established and a bimodal distribution results. Specimens from samples 1-3 (western and southern México except most of Chiapas) have unequal upper incisors, the outer pair the larger,

TABLE 5.—Qualitative cranial characters examined in five species of *Glossophaga*. The number of individuals exhibiting each character state is followed by the percent of total individuals examined in parentheses.

Species	Sex	N	Pterygoid alae					
			Absent		Modestly developed		Well developed	
<i>G. commissarisi</i>	M	138	121	(87.7)	10	(7.3)	7	(5.1)
	F	156	139	(89.1)	15	(9.6)	2	(1.3)
<i>G. leachii</i>	M	71	3	(4.2)	18	(25.4)	50	(70.4)
	F	58	6	(10.3)	9	(15.5)	43	(74.1)
<i>G. longirostris</i>	M	94	80	(85.1)	5	(5.3)	9	(9.6)
	F	108	95	(88.0)	8	(7.4)	5	(4.6)
<i>G. morenoi</i>	M	41	27	(65.9)	13	(31.7)	1	(2.4)
	F	26	16	(61.5)	10	(38.5)	0	
<i>G. soricina</i>	M	401	13	(3.2)	66	(16.5)	322	(80.3)
	F	410	15	(3.7)	74	(18.1)	321	(78.3)

Presphenoid ridge								
			Incomplete		Not prominent		Prominent	
<i>G. commissarisi</i>	M	137	118	(86.1)	14	(10.2)	5	(3.7)
	F	157	140	(89.2)	14	(8.9)	3	(1.9)
<i>G. leachii</i>	M	72	0		0		72	(100.0)
	F	58	0		2	(3.5)	56	(96.6)
<i>G. longirostris</i>	M	95	7	(7.4)	21	(22.1)	67	(70.5)
	F	108	4	(3.7)	24	(22.2)	80	(74.1)
<i>G. morenoi</i>	M	41	32	(78.1)	9	(22.0)	0	
	F	27	19	(70.4)	7	(25.9)	1	(3.7)
<i>G. soricina</i>	M	410	2	(0.5)	14	(3.4)	394	(96.1)
	F	415	2	(0.5)	14	(3.4)	399	(96.1)

Upper incisor angle								
			Greatly procumbent		Procumbent		Not procumbent	
<i>G. commissarisi</i>	M	136	4	(2.9)	7	(5.2)	125	(91.9)
	F	150	3	(2.0)	16	(10.7)	131	(87.3)
<i>G. leachii</i>	M	68	2	(2.9)	15	(22.1)	51	(75.0)
	F	56	2	(3.6)	14	(25.0)	40	(71.4)
<i>G. longirostris</i>	M	90	85	(94.4)	5	(5.6)	0	
	F	104	96	(92.3)	8	(7.7)	0	
<i>G. morenoi</i>	M	39	31	(79.5)	6	(15.4)	2	(5.1)
	F	28	22	(78.6)	5	(17.9)	1	(3.6)
<i>G. soricina</i>	M	389	300	(77.1)	87	(22.4)	2	(0.5)
	F	412	359	(87.1)	52	(12.6)	1	(0.2)

TABLE 5.—Continued.

Species	Sex	N	Upper incisor size						
			Not		Subequal		Equal		
			equal						
<i>G. commissarisi</i>	M	136	38	(27.9)	21	(15.4)	77	(56.6)	
	F	149	45	(30.2)	28	(18.8)	76	(51.0)	
<i>G. leachii</i>	M	68	16	(23.5)	19	(27.9)	33	(48.5)	
	F	55	22	(40.0)	12	(21.8)	21	(38.2)	
<i>G. longirostris</i>	M	90	15	(16.7)	20	(22.2)	55	(61.1)	
	F	104	32	(30.8)	19	(18.3)	53	(51.0)	
<i>G. morenoi</i>	M	38	31	(81.6)	6	(15.8)	1	(2.6)	
	F	27	22	(81.5)	4	(14.8)	1	(3.7)	
<i>G. soricina</i>	M	390	385	(98.7)	4	(1.0)	1	(0.3)	
	F	410	404	(98.5)	3	(0.7)	3	(0.7)	
			Lower incisors						
			Small and spaced		Small and paired		Medium-sized		Large
<i>G. commissarisi</i>	M	136	98	(72.1)	26	(19.1)	12	(8.8)	0
	F	154	101	(65.6)	33	(21.4)	19	(12.3)	1 (0.7)
<i>G. leachii</i>	M	69	3	(4.4)	2	(2.9)	53	(76.8)	11 (15.9)
	F	52	0		3	(5.8)	44	(84.6)	5 (9.6)
<i>G. longirostris</i>	M	91	0		0		10	(11.0)	81 (89.0)
	F	97	0		0		11	(11.3)	86 (88.7)
<i>G. morenoi</i>	M	38	0		0		38	(100.0)	0
	F	26	1	(3.9)	1	(3.9)	24	(92.3)	0
<i>G. soricina</i>	M	402	1	(0.3)	0		17	(4.2)	384 (95.5)
	F	404	0		0		17	(4.2)	387 (95.8)
			P3:P4 bulk						
			Not		Subequal		Equal		
			equal						
<i>G. commissarisi</i>	M	137	129	(94.2)	8	(5.8)	0		
	F	155	153	(98.7)	2	(1.3)	0		
<i>G. leachii</i>	M	71	66	(93.0)	5	(7.0)	0		
	F	59	50	(84.8)	7	(11.9)	2	(3.4)	
<i>G. longirostris</i>	M	95	42	(44.2)	37	(39.0)	16	(16.8)	
	F	110	51	(46.4)	48	(43.6)	11	(10.0)	
<i>G. morenoi</i>	M	41	24	(58.4)	14	(34.2)	3	(7.3)	
	F	28	16	(57.1)	12	(42.9)	0		
<i>G. soricina</i>	M	416	409	(98.3)	7	(1.7)	0		
	F	419	411	(98.1)	7	(1.7)	1	(0.2)	

TABLE 5.—Continued.

			Basisphenoid pits							
Species	Sex	N	Moderately							
			Shallow		deep		Deep			
<i>G. commissarisi</i>	M	137	7	(5.1)	74	(54.0)	56	(40.9)		
	F	156	4	(2.6)	83	(53.2)	69	(44.2)		
<i>G. leachii</i>	M	71	11	(15.5)	46	(64.8)	14	(19.7)		
	F	58	5	(8.6)	42	(72.4)	11	(19.0)		
<i>G. longirostris</i>	M	95	8	(8.4)	42	(44.2)	45	(47.4)		
	F	105	12	(11.4)	44	(41.9)	49	(46.7)		
<i>G. morenoi</i>	M	41	15	(36.6)	20	(48.8)	6	(14.6)		
	F	27	5	(18.5)	17	(63.0)	5	(18.5)		
<i>G. soricina</i>	M	403	148	(36.7)	201	(49.9)	54	(13.4)		
	F	407	175	(43.0)	188	(46.2)	44	(10.8)		

			Slope of rostrum							
			Continuous		Gradual		Moderate		Abrupt	
<i>G. commissarisi</i>	M	139	2	(1.4)	103	(74.1)	33	(23.7)	1	(0.7)
	F	157	4	(2.6)	134	(85.4)	19	(12.1)	0	
<i>G. leachii</i>	M	72	0		12	(16.7)	42	(58.3)	18	(25.0)
	F	59	0		17	(28.8)	33	(55.9)	9	(15.3)
<i>G. longirostris</i>	M	95	33	(34.7)	62	(65.3)	0		0	
	F	108	51	(47.2)	57	(52.8)	0		0	
<i>G. morenoi</i>	M	41	5	(12.2)	31	(75.6)	5	(12.2)	0	
	F	28	6	(21.4)	21	(75.0)	1	(3.6)	0	
<i>G. soricina</i>	M	419	31	(7.4)	299	(71.4)	88	(21.0)	1	(0.2)
	F	428	70	(16.4)	311	(72.7)	46	(10.8)	1	(0.2)

			Posterior palatine processes							
			Absent		Poorly developed		Moderately developed		Greatly developed	
<i>G. commissarisi</i>	M	139	70	(50.4)	48	(34.5)	20	(14.4)	1	(0.7)
	F	157	57	(36.3)	71	(45.2)	28	(17.8)	1	(0.6)
<i>G. leachii</i>	M	73	8	(11.0)	36	(49.3)	14	(19.2)	15	(20.6)
	F	58	8	(13.8)	27	(46.6)	15	(25.9)	8	(13.8)
<i>G. longirostris</i>	M	95	11	(11.6)	48	(50.5)	16	(16.8)	20	(21.1)
	F	109	11	(10.1)	61	(56.0)	14	(12.8)	23	(21.1)
<i>G. morenoi</i>	M	41	2	(4.5)	17	(41.5)	12	(29.3)	10	(24.4)
	F	28	2	(7.1)	15	(53.6)	5	(17.9)	6	(21.4)
<i>G. soricina</i>	M	415	40	(9.6)	214	(51.6)	101	(24.3)	60	(14.5)
	F	424	44	(10.4)	206	(48.6)	114	(26.9)	60	(14.2)

whereas individuals from the remaining samples (4-10) have upper incisors that usually are equal in bulk.

The size and positioning of the lower incisors in *G. commissarisi* exhibit little geographic variation. Most individuals have small, peglike lower incisors that are evenly spaced (68.6 percent) or with a larger diastema between the inner pair (20.3 percent) resulting in paired incisors on each mandibular ramus. Thirty-one of 290 (10.7 percent) individuals possess lower incisors that are medium in size; 17 of these specimens are from Costa Rica and Panamá (8-9). The single female from southern Colombia (10) has large lower incisors that are in contact with each other.

In *G. commissarisi*, the upper premolars are typically unequal in bulk (96.6 percent), the second being larger than the first. Ten of 292 (3.4 percent) individuals possess subequal premolars but no geographic trend is obvious. No specimens have premolars that are unequal in bulk.

Basisphenoid pits are deep (42.7 percent) or moderately deep (53.6 percent) in *G. commissarisi*. Specimens from southern Guatemala and southern Colombia (5, 10) tend to have shallower pits, and individuals from El Salvador, Honduras, and Nicaragua (6-7) possess deeper basisphenoid pits relative to specimens from other samples (1-4, 8-9).

The slope from the rostrum to the braincase is gradual (80.1 percent) or moderate (17.6 percent) in *G. commissarisi*. Specimens from southern México, Guatemala, Belize, El Salvador, Honduras, and Nicaragua (3-7) tend to possess a more pronounced rostral slope, particularly in Chiapas, Belize, and Guatemala (4-5), than specimens from other samples (1-2, 8-10).

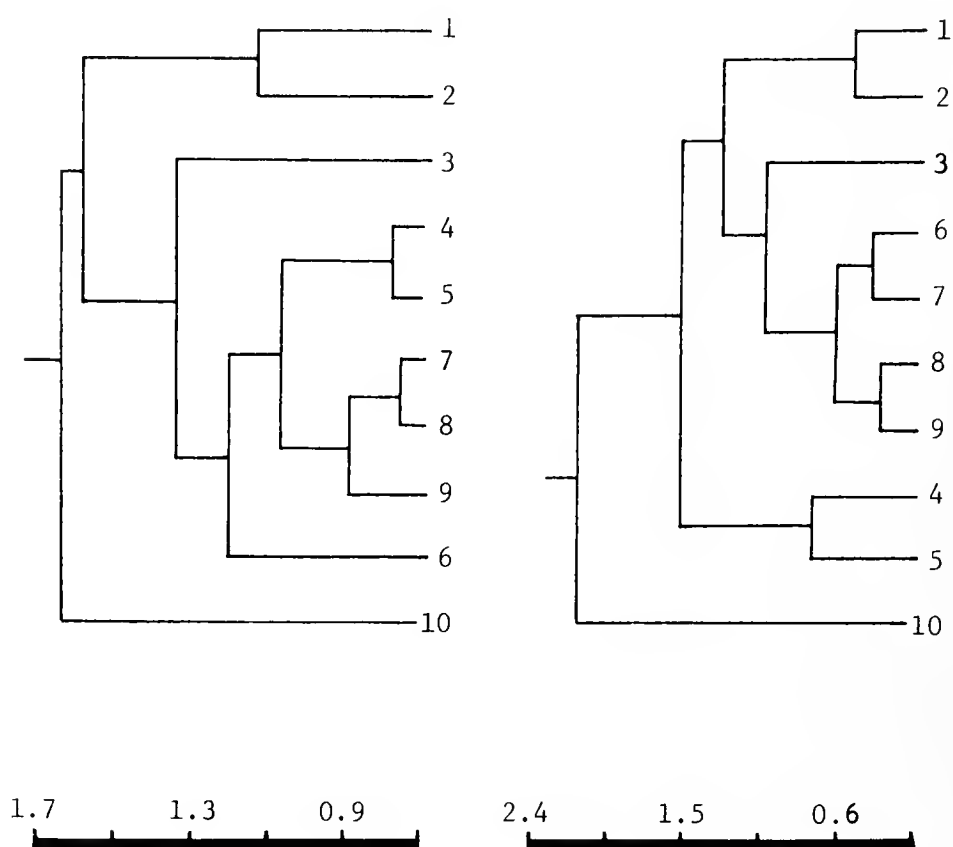
Posterior palatine processes are absent (42.9 percent) or poorly developed (40.2 percent) in *G. commissarisi*, especially in specimens from southern Guatemala to Panamá (5-9). Moderately developed processes are uncommon (16.2 percent) and most often found in individuals from México (Jalisco, Colima, Veracruz, Oaxaca, and Chiapas), northern Guatemala, and Belize (2-4).

Multivariate Analysis

The 16 external and cranial measurements, color, and nine qualitative cranial characters were analyzed using the NT-SYS programs, and phenograms were computed on both distance and correlation matrices to display phenetic relationships of males and females of *Glossophaga commissarisi*. Distance phenograms are presented herein because they have larger coefficients of cophenetic correlation (Fig. 2). Selected distance coefficients between adjacent samples for each sex also are included (Fig. 3).

The distance phenogram for male *G. commissarisi* indicates that the samples cluster into three major groups. Individuals from western México (1-2) form a group that is characterized by large size both externally and cranially. The two specimens from southern Colombia (10) represent another phenetically distinct

FIG. 2.—Distance phenograms for 10 samples of *Glossophaga commissarisi*. Phenograms were computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages for males (left) and females (right). The cophenetic coefficient of correlation for the phenograms for males is 0.828 and for females is 0.943. See Figure 1 and text for key to samples.



group that is also large in external and some cranial measurements (those reflecting length of skull), but they have narrower skulls than specimens from western México. The third group includes populations from southern México to Panamá, which cluster into four units: 1) Veracruz, Oaxaca, and western Chiapas (3); 2) southern México, Belize, and Guatamala (4-5); 3) Nicaragua, Costa Rica, and Panamá (7-9); and 4) El Salvador and Honduras (6). Specimens in the latter are somewhat larger than those in the first three in measurements of cranial length.

The distance phenogram for females shows samples falling into three major groups that are similar to those discussed in the preceding paragraph. The single specimen from southern Colombia (10) is phenetically distinct in several qualitative cranial characters, particularly the size and positioning of the upper and lower incisors, and is large both externally and in measurements of cranial width. Specimens from southern México and Guatamala (4-5) comprise the second group; bats in these populations are small cranially, particularly in measurements of cranial length. The third group includes those remaining populations from México to Panamá that tend to cluster into three smaller units: samples 1-2 (western México); 3 (Veracruz, Oaxaca, and western Chiapas); and 6-9 (El Salvador, Honduras, Nicaragua, Costa Rica, and Panamá). Specimens from samples 1-2 tend to be larger externally and cranially, whereas those in 3 and 6-9 average in the middle of the range for the species in most measurements; bats from samples 1-3 are further characterized by a deeper braincase relative to those in samples 6-9.

The first four principal components were computed from the correlation matrix among the 26 characters of the 10 samples based on the matrix of correlation among characters for both males and females. The first four principal components com-

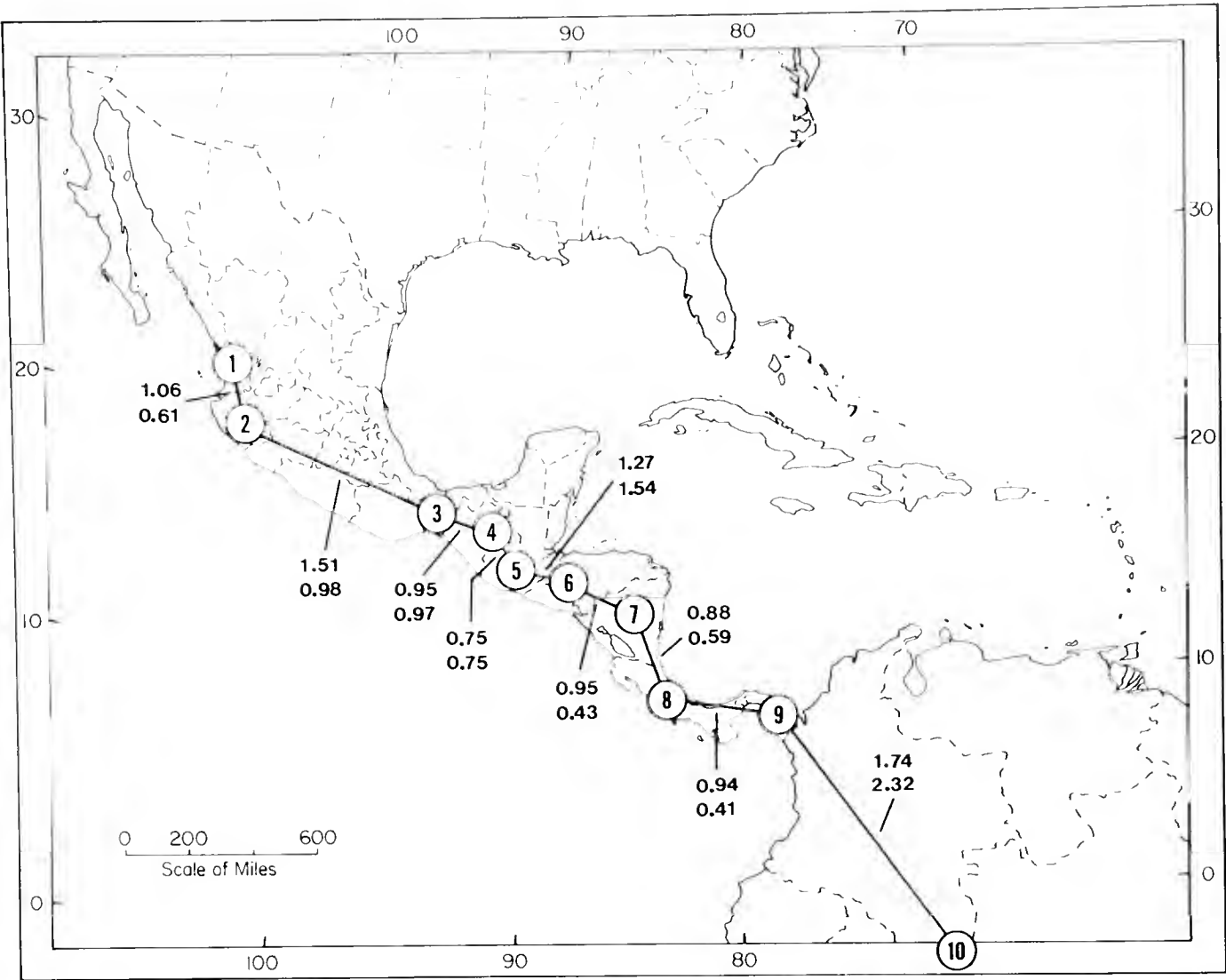


FIG. 3.—Selected distance coefficients between adjacent samples of *Glossophaga commissarisi*. Coefficients are from distance matrices for males (above) and females (below). See Figure 1 and text for key to samples.

bine to express 84.3 percent of the phenetic variation in males and 96.1 percent in females. The amount of phenetic variation represented in the first four principal components for males and females, respectively, was 42.9 and 45.0 for component I, 21.1 and 34.6 for component II, 12.5 and 11.6 for component III, and 7.8 and 4.9 for component IV. Two-dimensional plots of principal components I-II are presented for both sexes (Fig. 4). Characters with loading above 0.60 (or below -0.60) on any of the first four principal components are shown in Table 6.

OTUs of male *G. commissarisi* on the right-hand side of component I (samples 1-2, 10) are larger than average for the species in measurements of the wing, length of maxillary and mandibular toothrows, and breadth of braincase, whereas that to the left-hand side (sample 3) averages smaller in these dimensions. Upper incisor size and other measurements of cranial width and depth load heavily on component II for male *G. commissarisi*. OTUs to the bottom (samples 3-10) have narrow skulls and possess upper incisors that are equal in bulk; those to the top of component II (samples 1-2) are broad cranially and the upper incisors are unequal in bulk, the outer pair the larger.

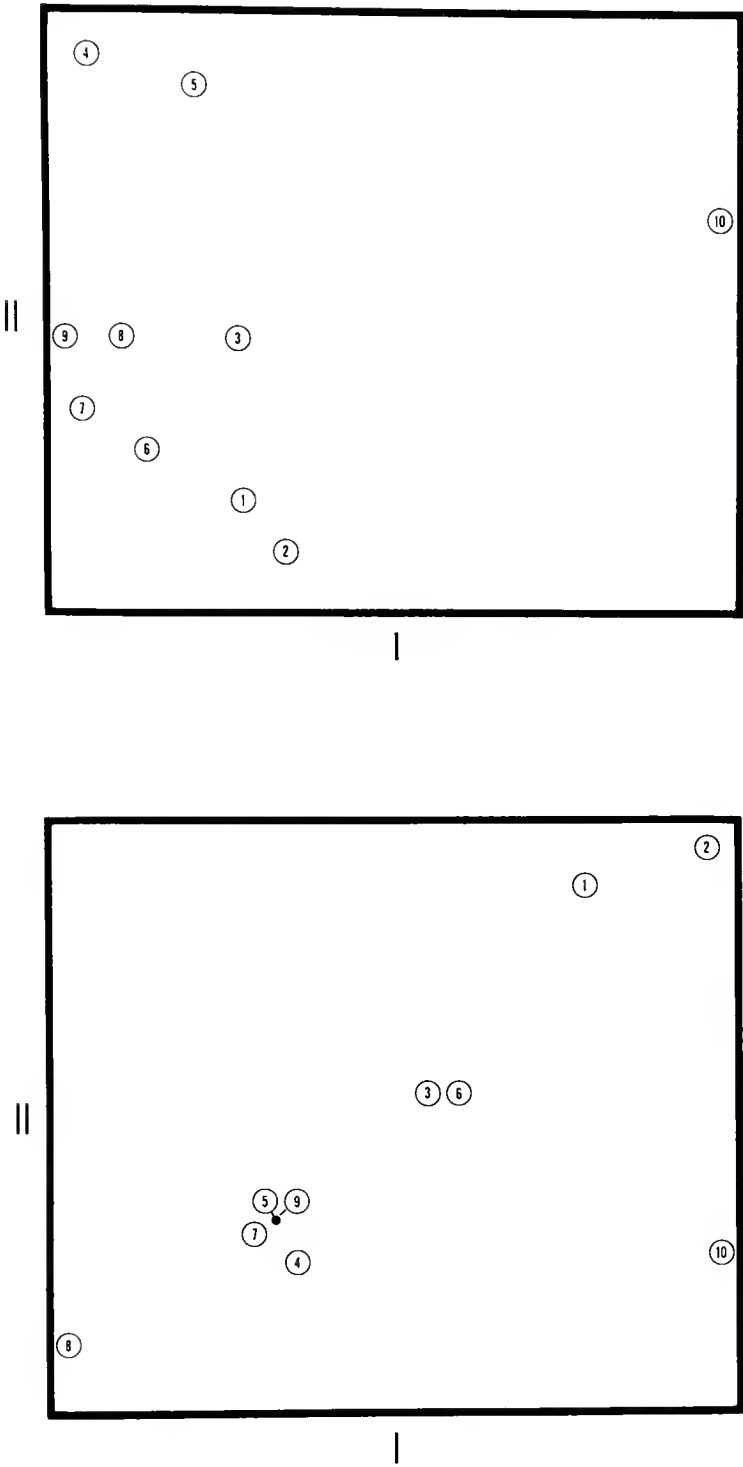


FIG. 4.—Two-dimensional plots for 10 samples of *Glossophaga commissarisi*. Component I plotted against component II for males (top) and females (bottom). See Figure 1 and text for key to samples.

The two-dimensional plot of female *G. commissarisi* is different from that of males. Wing measurements and several qualitative cranial characters load heavily on component I so that the OTU to the right-hand side (sample 10) is larger externally, the presphenoid ridge is better developed, the upper incisors are more procumbent and unequal in size (the outer pair the larger), the lower incisors are larger, and the postpalatal processes are better developed. Specimens from samples 1-9, plotted on the left-hand side of component I, are smaller externally, have a poorly developed presphenoid ridge and postpalatal processes, smaller lower incisors, and the upper incisors are not noticeably procumbent. Measurements of cranial length and some of cranial width (zygomatic breadth, interorbital breadth, and width across molars) load heavily on component II. Specimens from samples 4-5 are smaller than average for the species in these measurements, whereas those from samples 1-2 average larger.

TABLE 6.—*Factor loadings for 26 characters examined in Glossophaga commissarisi. Only loadings above 0.600 (or below -0.600) on the first four principal components are shown (males above, females below).*

Character	I	II	III	IV
Length of forearm	0.894			
	0.847			
Length of third metacarpal	0.875			
	0.950			
Length of fourth metacarpal	0.920			
	0.968			
Length of fifth metacarpal	0.904			
	0.958			
Greatest length of skull	0.770	-0.941		
Condylobasal length	0.903			
	-0.841			
Zygomatic breadth		0.809		
		-0.772		
Length of rostrum		0.658		
		-0.944		
Mastoid breadth		0.607		
		-0.694		
Interorbital breadth		0.762		
		-0.738		
Breadth of braincase	0.909		0.955	
Depth of braincase		0.698		
	0.714		0.600	
Length of maxillary toothrow	0.802	-0.985		
Length of mandibular toothrow	0.873	-0.979		
Width across molars		0.796		
		-0.831		
Mandibular length				0.737
		-0.810		
Pelage coloration	-0.703			
	-0.791			
Pterygoid alae				
	-0.762			
Presphenoid ridge				
	-0.786			
Lower incisors			0.727	
	0.726		-0.648	
Upper incisor angle			-0.865	
	-0.855			
Upper incisor size		-0.704		
	-0.909			

TABLE 6.—Continued.

Character	I	II	III	IV
Basisphenoid pits				0.850
	-0.682			
P3:P4 bulk				
	-0.811			
Rostral slope				-0.781
		0.611	0.662	
Postpalatal processes			0.879	
	0.959			

Taxonomic Conclusions

Patterns of geographic variation and the disjunct distribution of *Glossophaga commissarisi* indicate that three well-defined subspecies exist. The isolated race of relatively large bats that is known from Sinaloa and Durango southward to Colima is phenetically distinct and probably does not intergrade with populations found farther south in México and Central America. To this race from western México, the trinomial *Glossophaga commissarisi hespera* Webster and Jones applies. The nominate subspecies, *Glossophaga commissarisi commissarisi* Gardner, is known from southern México southeastward at least to Panamá, and may be expected in western Colombia as well. This race varies geographically in that specimens from El Salvador and Honduras are moderately large but those to the adjacent northwest and southeast become relatively smaller in parameters that reflect cranial length. Overall patterns in variation, however, do not indicate any zones of reduced gene flow and no hiatus in the geographic distribution is apparent. Specimens from the upper Amazon Basin are characterized by being larger than average for the species in measurements of the wing and length of cranium but smaller than average in parameters that reflect cranial width, and the name *Glossophaga commissarisi bakeri* Webster and Jones is applicable to this subspecies.

Glossophaga commissarisi bakeri Webster and Jones

1987. *Glossophaga commissarisi bakeri* Webster and Jones, Occas. Papers Mus., Texas Tech Univ., 109:2, 3 September.

Holotype.—Adult male, skull removed from fluid preserved specimen, TTU 9093, from Isla Santa Sofia, 30 km. NW Leticia, Amazonas, Colombia; obtained on 28 June 1969 by R. J. Baker, original no. 1453. Holotype examined; skin (in alcohol) in excellent condition except right humerus removed; skull in good condition, upper third molars absent (alveoli present), zygoma broken, and right otic capsule partially damaged.

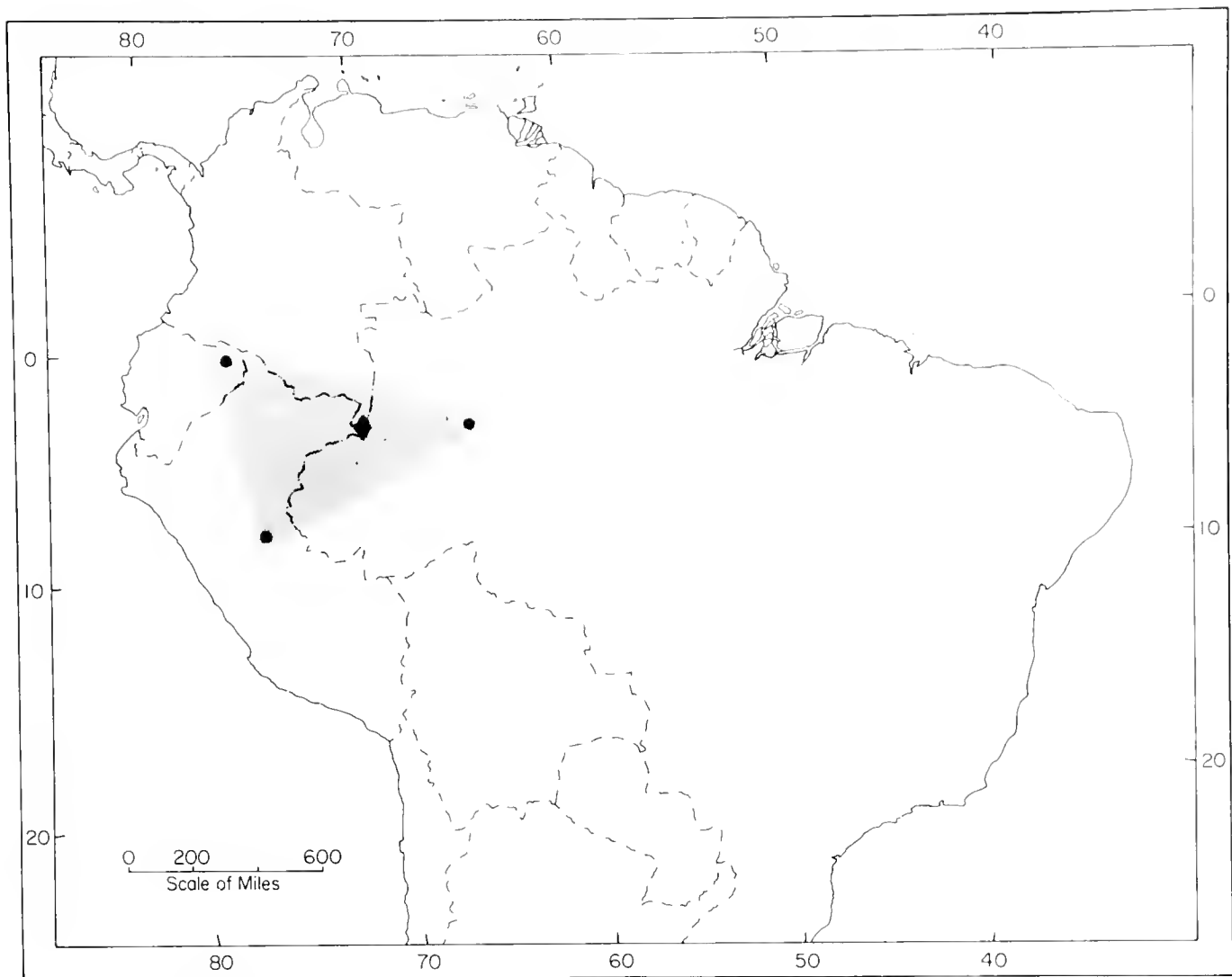


FIG. 5.—Geographic distribution of *Glossophaga commissarisi bakeri*. Circles represent marginal localities and the diamond represents the type locality.

Measurements of the holotype (external measurements taken from fluid preserved specimen).—Total length, —; length of tail, 5; length of hind foot, 10; length of ear from notch, 12; length of forearm, 34.0; greatest length of skull 20.1; condylobasal length, 18.5; zygomatic breadth, 9.3; mastoid breadth, 9.0; interorbital breadth, 4.1; length of mandibular toothrow (c-m3), 7.2.

Distribution.—This race currently is known from southern Colombia, eastern Ecuador, eastern Perú, and western Brazil (Fig. 5), but it may be more widespread in the upper Amazon Basin; known from less than 300 meters in elevation.

Comparisons.—*Glossophaga commissarisi bakeri* is distinguished from *G. c. commissarisi* and *G. c. hespera* in that the presphenoid ridge is better developed (rather than noticeably flattened subterminally), the parastyle of M1 is reduced (rather than better developed and directed posterolabially), the upper and lower molars are relatively larger, and the lower incisors are subequal in size (rather than unequal, the outer pair the larger). Quantitatively, *G. c. bakeri* differs from *G. c. commissarisi* in being large in most external and cranial dimensions and approaches the relatively large size of *G. c. hespera*; however, *G. c. bakeri* averages smaller than *G. c. hespera* in measurements of cranial width.

Reproduction.—Females collected on 28 May and 8 August each carried one fetus with crown-rump lengths of 16.2 and 12, respectively, and another taken on 28 June evinced no reproductive activity; a male taken on 24 October had enlarged testes (Webster and Jones, 1987).

Specimens examined (7).—BRAZIL. *Amazonas*: Lago de Tefe, 2 (USNM). COLOMBIA. *Amazonas*: Isla Santa Sofia, 30 km. NW Leticia, 3 (TTU). PERU. *Loreto*: Iquitos, 1 (TCWC); 11 mi. SE Pucallpa, 500 ft., 1 (TCWC).

Additional records.—ECUADOR. *Napo*: Límon Cocha (Albuja, 1983). PERU. *Loreto*: San Lorenzo, Río Marañón, 500 ft. (Handley, personal communication, see Webster and Jones, 1987).

Marginal records.—ECUADOR. *Napo*: Límon Cocha. BRAZIL. *Amazonas*: Lago de Tefe. PERU. *Ucayali*: 11 mi. SE Pucallpa, 500 ft. *Loreto*: San Lorenzo, Río Marañón, 500 ft.

Glossophaga commissarisi commissarisi Gardner

1962. *Glossophaga commissarisi* Gardner, Los Angeles Co. Mus., Contrib. Sci., 54:1, 11 May.

Holotype.—Adult male, skin and skull, LACM 14130, from 10 km. SE Tonalá, Chiapas, México; obtained on 1 August 1961 by A. L. Gardner, original no. 3251. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Total length, 63; length of tail, 8; length of hind foot, 9; length of ear from notch, 14; length of forearm (dry), 33.3; greatest length of skull, 20.3; condylobasal length, 18.5; zygomatic breadth, 9.8; mastoid breadth, 9.3; interorbital breadth, 4.0; length of maxillary toothrow, 6.7; length of mandibular toothrow (c-m3), 7.1; weight, 10 grams.

Distribution.—This subspecies occurs throughout much of southeastern México (excluding the Yucatán Peninsula) and Central America (Fig. 6); known altitudinal distribution is from near sea level to 2000 meters in elevation. The northwestern limit of the range of *G. commissarisi* is in Veracruz and eastern Oaxaca and the southern limit is in eastern Panamá; however, the subspecies probably occurs in western Colombia as well.

Comparisons.—*Glossophaga commissarisi commissarisi* is distinguished from *G. c. hespera* and *G. c. bakeri* by its smaller size externally and cranially, and average darker color of pelage. The angle between the rostrum and cranium is less abrupt, the braincase is less domed, and the posterior extension of the presphenoid is well developed and noticeably raised (in ventral view) from the basisphenoid septum in the nominate subspecies, whereas in *G. c. hespera* the posterior presphenoid extension is poorly developed and continuous with the basisphenoid septum. Further comparisons between *G. c. commissarisi* and *G. c. bakeri* are in the accounts of those subspecies.

Reproduction.—There is little published information dealing with the reproductive patterns in *G. commissarisi* (see Wilson, 1979). I recorded the reproductive condition of 231 females from throughout the geographic range of *G. c. commissarisi* and calculated the percent pregnant and lactating each month (Fig. 7). In ad-

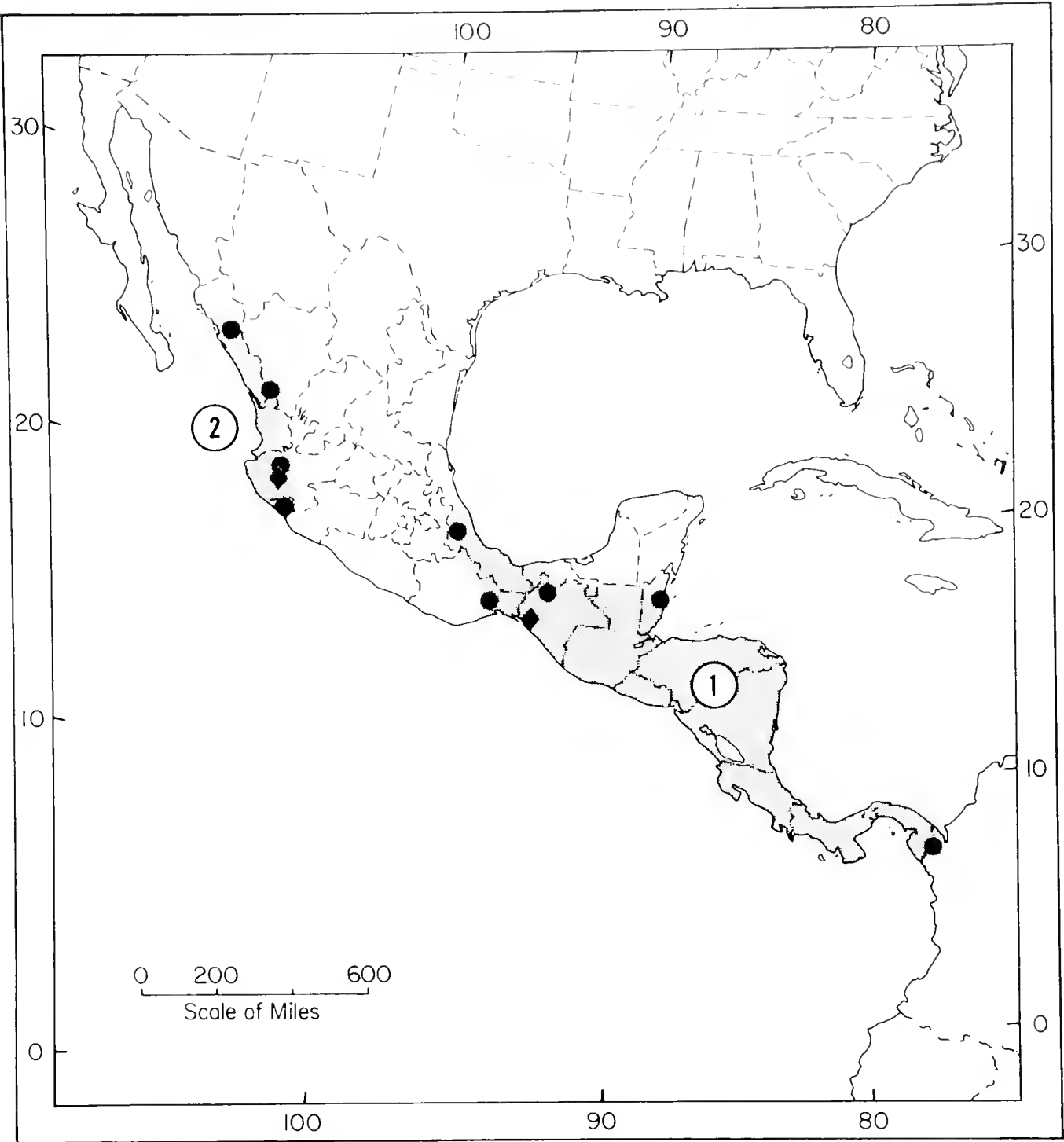


FIG. 6.—Geographic distribution of *Glossophaga commissarisi commissarisi* (1) and *Glossophaga commissarisi hespera* (2). Circles represent marginal localities and diamonds represent type localities.

dition, testicular length was averaged for 78 males from throughout the geographic range of *G. c. commissarisi*; these are also shown in Figure 7. Percents were not figured if fewer than five individuals of each sex per month were available.

Two peaks in parturition are evident, a large one from January to April and a smaller one in July and August. Lactation is most frequently observed in April and May. Testicle size increases from January to May and decreases from May until August. Reproductive patterns from September through December are unclear, too few individuals being available from those months. The reproductive strategy of *G. c. commissarisi* appears to be one of monotocous bimodal polyestry with a

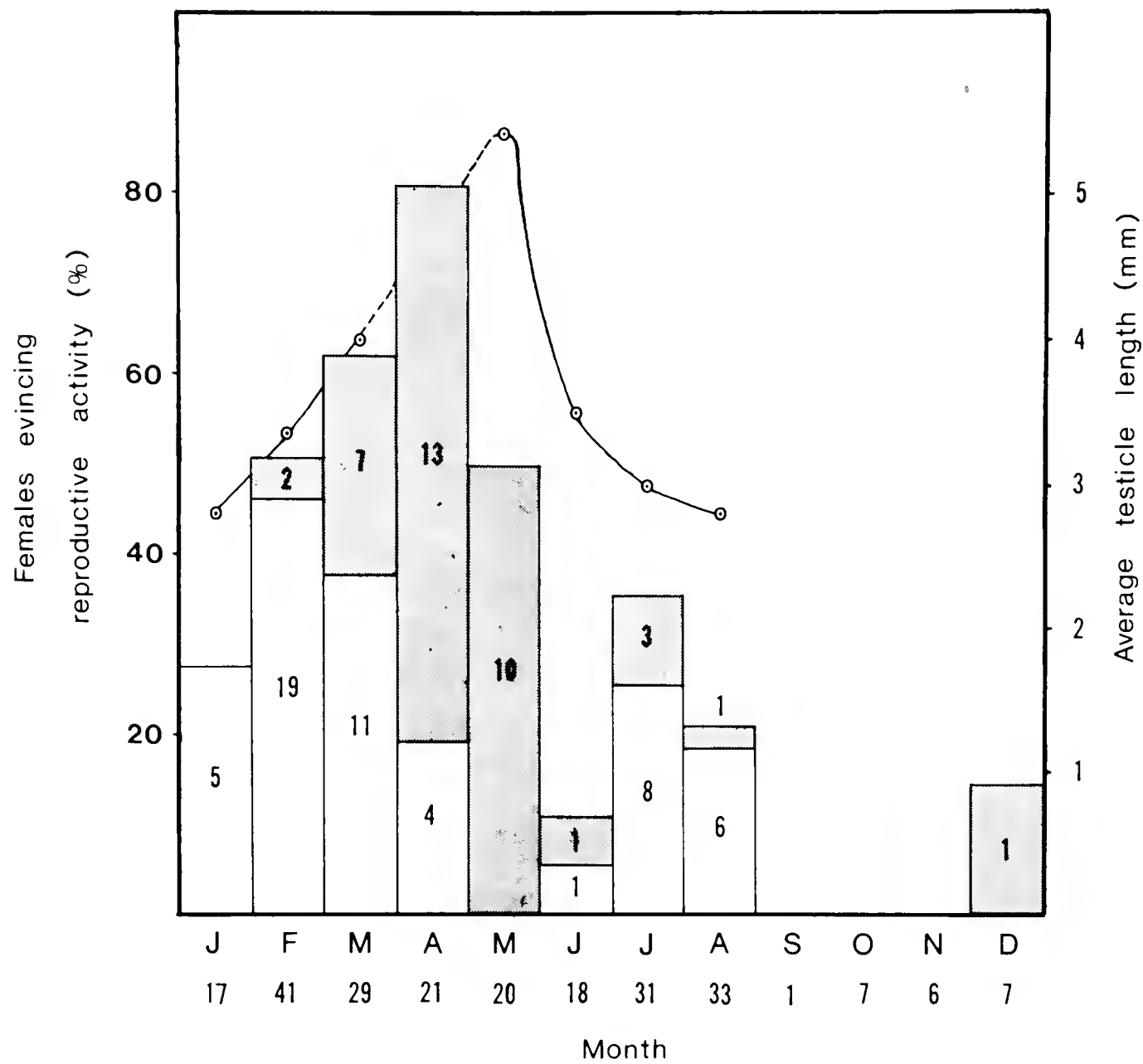


FIG. 7.—Reproductive activity in *Glossophaga commissarisi commissarisi*. The histogram represents the percent of 231 females evincing pregnancy (open) or lactation (stipple) each month; the number of pregnant and lactating females are in the histogram, and the total number of females examined are shown below each month. Average length of testes is plotted for several months. Reproductive data are not included for months in which fewer than five individuals of each sex are available.

postpartum estrus, and is similar to the pattern seen in *Artibeus jamaicensis* in Panamá (Fleming, 1971).

Remarks.—Average external measurements (extremes in parentheses) of 105 males followed by those of 103 females of *G. c. commissarisi* are: total length, 59.1 (46-69), 59.6 (40-72); length of tail, 6.5 (1-11 in 92 specimens), 7.0 (4-11 in 93 specimens); length of hind foot, 10.2 (7-13), 10.4 (6-15); length of ear from notch, 13.5 (6-17), 13.4 (5-18).

Specimens examined (623).—BELIZE. *Belize*: Rockstone Pond, 5 (ROM). *Toledo*: Aguacate Village, 1 (FMNH); Forest Home, 1 (FMNH); Lubaantun, 1 (FMNH); 0.2 mi. E Wilson Rd., 1 (FMNH). *No locality*: 2 (UMMZ). COSTA RICA. *Alajuela*: Los Chiles, 2 (LACM); Playuelas, 1

(LACM). *Cartago*: Pacuare, 3 (LSU). *Guanacaste*: 4 mi. NW Cañas, Finca la Pacífica, 1 (MSB); 9 mi. S Cañas, 35 m., 9 (UMMZ); 6 mi. S, 6 mi. W Cañas, Finca Jiménez, 11 m., 4 (UMMZ); 7 mi. SW Philadelphia, 7 (KU); 3 mi. E Tilaran, 950 m., 7 (LSU). *Heredia*: ca. Puerta Viejo, 4 (1 KU, 1 LSU, 2 UMMZ). *Limón*: Cariari, 4 (LSU); Finca la Lola, 2 (LACM); Jiménez, 600-1000 ft., 1 (AMNH); Río Sixaola (Sicsola), 1 (AMNH). *Puntarenas*: Boca de Río Barranca, 1 (LACM); Julieta, Finca la Ligia, 1 (LSU); Monte Verde, 2 (LACM); Palmar (Pacífica), 250 ft., 1 (AMNH); Rincón de Osa, sea level, 2 (LSU); San Francisco Esparata, ca. 1000 ft., 1 (AMNH). *San José*: Río Carragres, 2 (LSU); San Gerónimo Pirris, 1 (AMNH). EL SALVADOR. *Chalatenango*: 20 km. W Chalatenango, 250 m., 9 (TCWC). *Cuscatlán*: 14 km. NE Suchitoto, 250 m., 5 (TCWC). *La Libertad*: 8.4 mi. NW Colón, 6 (TTU); 3.5-5.1 km. E La Libertad, 15 m., 6 (TCWC); 16.8-20 km. W La Libertad, 30-250 m., 3 (TCWC). *San Salvador*: San Salvador, 1 (KU). GUATAMALA. *Alta Verapaz*: Los Rápidos (Río Icuolay) 1 (AMNH); San Cristobál Verapaz, 1380 m., 6 (TCWC). *Baja Verapaz*: 1 km. SE San Jerónimo, 1000 m., 5 (TCWC); San Miguel Chicaj, 750 m., 1 (TCWC). *Chimaltenango*: Yepocapa, 1 (FMNH). *Escuintla*: 6 mi. S Democracia, 1 (FMNH); 2 mi. S Palín, 4000 ft., 5 (TCWC); Río Bravo, 1 (FMNH); San Jose, 1 (FMNH). *Guatemala*: Amatitlán, 3800 ft., 1 (TCWC). *Huehuetenango*: La Democracia, 3300 ft., 2 (TCWC). *Izabal*: 25 km. SSW Puerto Barrios, 300 ft., 13 (TCWC). *Jutiapa*: 6 mi. S Ascunción Mita, 2000 ft., 10 (TCWC); 15 km. NE Jutiapa, 3000 ft., 1 (TCWC); Montúfar, El Paraíso, 1 (AMNH). *Petén*: Altar de Sacrificios (near Río de la Pasión), 1 (AMNH). *Quezaltenango*: 8 km. E Coatepeque, 2200 ft., 2 (TCWC); 1 km. S Santa Maria, 4700 ft., 1 (TCWC). *Quiché*: 1 km. WNW Sacapulas, 1200 m., 1 (TCWC). *Retahuleu*: 3 km. N Retahuleu, 1000 ft., 2 (TCWC); 15 km. SW Retahuleu, 240 ft., 3 (TCWC). *San Marcos*: El Carmen, 1600 ft., 6 (TCWC); El Porvenir, 1 (FMNH); Hda. California, 3 (AMNH). *Santa Rosa*: Astillero, 25 ft., 2 (KU); 3 km. S, 6 km. E Cuilapa, 2400 ft., 1 (TCWC); Finca el Zapote, 7 (UMMZ); 2 km. ESE Ixpaco, 2 (AMNH); La Avellana, 9 (5 AMNH, 4 USNM); 12-13.5 km. N La Avellana, 3 (2 AMNH, 1 USNM). *Sololá*: Escobas, 1 (FMNH); Moca, 2 (FMNH); San Lucas, 2 (AMNH). HONDURAS. *Atlántida*: 0-2 km. SE Lancitilla, 40-150 m., 8 (TCWC); Tela, 1 (FMNH). *Choluteca*: 36 km. SE Choluteca, 600 m., 1 (TCWC). *Cortés*: Cofradía, 500 ft., 1 (AMNH). *El Paraíso*: Chichicasta, 480 m., 1 (TCWC); 7-8 km. E Danlí, 680 m., 8 (TCWC). *Francisco Morazán*: San Marcos de Guaymaca, 3000-3500 ft., 2 (AMNH). *Gracias A Dios*: 0-4 km. NE Brus Laguna, 4 (TCWC). *Olancho*: 40 mi. E Catacamas, 500 m., 6 (TCWC); Río Coco, 78 mi. ENE Danlí, 900 ft., 4 (TCWC). MEXICO. *Chiapas*: 5-8 mi. N Arriaga, 800-2500 ft., 5 (TCWC); 2 km. NE Cacahuatán (Cacahuetal), 1 (LACM); Caridad, 57 km. ESE Altamirano, 900 m., 1 (TCWC); 3 mi. E Cintalapa, 1700 ft., 1 (TCWC); 32 mi. SW Cintalapa, 4 (TTU); 24 km. W Cintalapa, 1 km. W Rancho San Miguel, 2 (UA); 11 km. NW Escuintla, ca. 100 ft., 2 (1 LACM, 1 UA); Huehuetán, 300 ft., 1 (USNM); ca. 17 km. N Huixtla, km. 184 on Hwy. 200, Puente Vado Ancho, 2 (UA); ca. 23.6 mi. NW Huixtla, 400 ft., 11 (8 TCWC, 3 TTU); 38 km. N Huixtla, ca. 100 ft., 1 (LACM); 2 mi. SE Huixtla, Río Tepozapa, 400 ft., 4 (TCWC); 33 mi. NE Las Margaritas, Finca Patichuiz, ca. 6000 ft., 2 (1 LACM, 1 UA); 12 mi. N Mapastepec, 3 (UA); 12 mi. E Ortiz Rubio, 1 (UA); 20 km. SE Pijijiapan, 1 (LACM); Puerto Madero, 5 m., 2 (KU); Sabana San Quintín, 215 m., 8 (KU); 15 km. SE San Clemente, Finca San Salvador, 1000 m., 1 (KU); 8 km. S Solusuchiapa, ca. 400 ft., 3 (LACM); 6.8 mi. N Tapachula, Hwy. 18, Rancho San George, 1 (TTU); 3.8 mi. SW Tapachula, Hwy. 18, 8 (TTU); ca. 9-21 km. SE Tonalá, 49 (37 LACM, 3 UMMZ, 4 TCWC, 2 TTU, 3 UA); 35 mi. SSE Tuxtla Gutiérrez, 2200 ft., 1 (TCWC); 10 mi. S Zapaluta, 3000 ft., 1 (ROM). *Oaxaca*: 0.5 mi. W Chiltepec, 10 (AMNH); 18-24 mi. N Matias Romero, 6 (1 AMNH, 4 LACM, 1 USNM); 6 mi. S Matias Romero, Río Grande, 1 (USNM); Santiago Lachiquirí, 2500 ft., 2 (AMNH); 4-5 mi. E Tapanatepec, ca. 800 ft., 9 (8 TCWC, 1 UA); 2.7 mi. W Tapanatepec, 300 ft., 3 (KU). *Veracruz*: 1.3 mi. NE Balzapote, 1 (TCWC); 33.9 km. ENE Catemaco, 100 m., 7 (TCWC); 35 km. ENE Jesús Carranza, 150 ft., 1 (KU); 2 mi. E Lago Catemaco, Río Quezalapan, 2 (TCWC); Mirador, 1 (USNM). NICARAGUA. *Boaco*: Los Cocas, 14

km. S Boaco, 1 (TTU); Santa Rosa, 17 km. N, 15 km. E Boaco, 300 m., 22 (KU). *Chinandega*: 10 km. S Chinandega, Hda. San Isidro, 1 (KU); El Realejo, Hda. San Isidro, 1 (USNM); 8 km. N, 4 km. E Posoltega, 1 (AMNH); 3 km. N Sabana Grande, 1 (KU); San Antonio, 9 (KU). *Chontales*: 6 km. E Mugán, 380 m., 3 (KU); 1 km. N, 2.5 km. W Villa Samoza, 1 (KU). *Granada*: 6.5 km. SE Guanacaste, Finca Santa Cecilia, 660 m., 1 (KU). *Madriz*: Darailí, 5 km. N, 14 km. E Condega, 940 m., 3 (KU). *Matagalpa*: La Danta, 1 km. N, 5 km. E Esquipulas, 780 m., 3 (KU); 10.5 km. N, 9 km. E Matagalpa, 960 m., 2 (KU); Santa María de Ostuma, 1250 m., 1 (KU). *Río San Juan*: 0-1 mi. S El Castillo, 40-130 m., 25 (TCWC). *Rivas*: 13 km. S, 14 km. E Rivas, Finca Amayo, 40 m., 1 (KU). *Zelaya*: Bonanza, 850 m., 5 (4 KU, 1 USNM); 50 mi. from Bluefields, Escondido River, 1 (USNM); Cara de Mono, 50 m., 1 (KU); Eden, 1 (ANSP); El Recreo, S side of Río Mico, 25 m., 16 (KU); Muelle de Los Bueyes, 100 ft., 1 (TCWC); 9 mi. E Rama, Dos Bocas, 1 (TTU); 10 km. W Rama, 40 m., 10 (TCWC); 3-4.5 km. NW Rama, ca. 100 m., 6 (3 TCWC, 3 TTU). PANAMA. *Bocas del Toro*: Almirante, 24 (USNM); Boca del Drago, 8 (USNM); Cayo Agua, Puerto Norte, 5 (USNM); Changena Camp, 1 (USNM); Sibube, 1 (USNM). *Canal Zone*: Buena Vista Peninsula, 1.75 km. NNW Frijoles, 1 (USNM). *Chiriquí*: 1 mi. E Cuestra de Piedra, 2800 ft., 3 (USNM); San Vincent, 1800 ft., 1 (USNM). *Coclé*: Santa Clara, 1 (USNM). *Colón*: Campo Sasardi, 4 mi. W Malatupo, 1 (MSU). *Darién*: Boca de Cupe, 4 (USNM); Boca de Río Paya, 7 (USNM); Jaqué, 23 (USNM); Tacarcuna Village Camp, 3200 ft., 9 (USNM). *Panamá*: Candelaria, 2 (USNM); Cerro Azul, 13 (USNM). *San Blas*: Armila, Quebrada Venado, 7 (USNM); Mandinga, 2 (USNM).

Additional records.—COSTA RICA. *Puntarenas*: 4 km. SW Rincón (LaVal, 1970); San Vito (Howell and Burch, 1974). EL SALVADOR (Hellebuyck *et al.*, 1985). *Ahuachapán*: Bosque El Imposible. *Santa Ana*: El Encinal, Distrito Forestal y Fauna, Metapan, on the slopes of Cerro Montecristo. GUATAMALA. *Sacatepequez*: 4.8 km. NE Antigua, 1935 m. (McCarthy and Bitar, 1983). *Santa Rosa*: Camalote (Dickerman *et al.*, 1981). MEXICO. *Chiapas*: 42 km. W Cintalapa (Baker, 1967); Reserva Ecológica El Triunfo, 17 km. SE Finca Prusia, 2000 m. (Medellín, 1988). NICARAGUA. *Zelaya*: 6 mi. W Rama, 50 ft. (Davis *et al.*, 1964). PANAMA. *Darién*: Paya Village (Handley, 1966).

Marginal records.—MEXICO. *Veracruz*: Mirador. *Chiapas*: 8 km. S Solusuchiapa, ca. 400 ft. BELIZE. *Belize*: Rockstone Pond. PANAMA. *Darién*: Tacarcuna Village Camp, 3200 ft. MEXICO. *Oaxaca*: Santiago Lachiquirí.

Glossophaga commissarisi hespera Webster and Jones

1982. *Glossophaga commissarisi hespera* Webster and Jones, Occas. Papers Mus., Texas Tech Univ., 76:2, 29 January.

Holotype.—Adult female, skin and skull, TTU 36223, from Tepehuajes Mine, ca. 20 km. N Soyatlán del Oro, Jalisco, México; obtained on 16 January 1964 by A. L. Gardner, original no. 6864. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Total length, 75; length of tail, 9; length of hind foot, 11; length of ear from notch, 13; length of forearm (dry), 35.6; greatest length of skull, 21.2; condylobasal length, 19.3; zygomatic breadth, 9.5; mastoid breadth, 9.2; interorbital breadth, 4.2; length of maxillary toothrow, 7.3; length of mandibular toothrow (c-m3), 7.7; weight, 12 grams.

TABLE 7.—Recorded reproductive activity in females of *Glossophaga commissarisi hespera*.

Month	Number examined	Number pregnant	Number lactating
January	6	4	0
February	4	1	0
March	1	0	0
April	7	2	0
May	8	2	1
June	-	-	-
July	11	1	0
August	-	-	-
September	1	1	0
October	-	-	-
November	2	0	0
December	4	0	0

Distribution.—This subspecies occurs in western México from central Sinaloa and southwestern Durango southward to western Jalisco and Colima (Fig. 6); known altitudinal distribution from near sea level to 2000 meters in elevation.

Comparisons.—*Glossophaga commissarisi hespera* is distinguished from *G. c. commissarisi* and *G. c. bakeri* by its larger size externally and cranially, especially in measurements of the wing and those that reflect cranial width (mastoid breadth, interorbital breadth, and width across molars). The braincase is more domed, the angle between the rostrum and cranium is more abrupt, and the posterior pre-sphenoid extension is small and continuous (in ventral view) with the basisphenoid septum in *G. c. hespera* (well developed and noticeably raised in ventral view in *G. c. commissarisi*). In addition, *G. c. hespera* averages paler in color than the nominate subspecies. Additional comparisons between *G. c. hespera* and *G. c. bakeri* are included in the accounts of those subspecies.

Reproduction.—The scanty information from 44 females of *G. c. hespera* (Table 7) is reminiscent of bimodal polyestry. Although it does not reinforce the monthly data for *G. c. commissarisi*, I suspect that the reproductive timing and not the strategy differs between the two.

Remarks.—Average external measurements (extremes in parentheses) of 12 males followed by those of 20 females of *G. c. hespera* are: total length, 59.8 (55-66), 63.5 (56-83); length of tail, 6.1 (3-9 in 11 specimens), 7.4 (5-11 in 19 specimens); length of hind foot, 10.3 (9-11.5), 10.1 (8-12); length of ear from notch, 14.8 (13-16), 13.8 (10-16).

Specimens examined (47).—MEXICO. *Colima*: Chirpas, Ocozocoautla, Cerro Brujo, El Cielito, 4500 ft., 1 (AMNH); Miscoate, 2 (LACM); 11 mi. W Comala, Miscoate, 4 (LACM); Pueblo Juárez, 1 (UA); 5 km. SE Pueblo Juárez, 1 (UA); 35 km. NW Pueblo Juárez, Rancho Tavernillas, 2 (UA); 1 km. S Pueblo Nuevo, 1 (UA); 2.5 km. NW Pueblo Nuevo, 1 (UA). *Durango*: 2 mi. N Pueblo Nuevo, 6000 ft., 1 (MSU); 6 mi. S Pueblo Nuevo, 3000 ft., 1 (MSU). *Jalisco*: 14 mi. WSW

Ameca, 5000 ft., 1 (KU); 8 km. ESE Chamela, 30 m., 1 (MSU); 6 mi. E El Limón, 2700 ft., 1 (KU); 2 mi. N Milpillas, 3000 ft., 1 (KU); 20 km. WNW Purificación, 1400 ft., 2 (KU); *ca.* 20 km. N Soyatlán del Oro, Tepehuajes Mine, 2 (1 TTU, 1 UA); 10 mi. SE Talpa de Allende, 5300 ft., 1 (KU); 7.5 mi. SE Tecomates, 1500 ft., 1 (KU). *Nayarit*: 4 km. S Aticama, 2 (USNM); Chacala, 2 (USNM); Jalcocotán, 1 (USNM); 1 mi. S San Marcos (Lo de Marcos), 2 (USNM); Paso de Soquipa (Zoquipa), 1 (USNM); Río Chilte, 1.2 mi. S El Casco, 480 ft., 1 (USNM); San Blas, 1 (AMNH); 5-11 mi. NE San Blas, *ca.* 500 ft., 2 (1 KU, 1 MSU); 4-8 mi. E San Blas, 4 (1 LACM, 1 MSU, 2 UA); 4 mi. S, 5 mi. E San Blas, 1 (MSB); 5 mi. SE San Blas, 1 (KU). *Sinaloa*: 20 km. N, 5 km. E Badiraquato, 1800 ft., 2 (KU); Santa Lucía, 3600 ft., 2 (KU).

Additional records.—MEXICO. *Colima*: Cerro Chino (Gardner, 1962); El Cóbano (Kennedy *et al.*, 1984). *Jalisco* (Watkins *et al.*, 1972): 11 mi. SW Autlán, 2000 ft.; 2 mi. S La Cuesta, 1500 ft.

Marginal records.—MEXICO. *Sinaloa*: 20 km. N, 5 km. E Badiraquato, 1800 ft. *Durango*: 2 mi. N Pueblo Nuevo, 6000 ft. *Jalisco*: 14 mi. WSW Ameca, 5000 ft. *Colima*: 5 km. SE Pueblo Juárez.

Glossophaga leachii Gray's Long-tongued Bat

This bat is continuously distributed along the Pacific versant and upper slopes of the Caribbean versant from central México (Colima, Jalisco, and Tlaxcala) southeastward to central Costa Rica; it is not known, however, from the mesic Caribbean lowlands or the arid Yucatán Peninsula.

Diagnosis

Relatively small in measurements of cranial length and breadth (particularly interorbital breadth), but extremely large in measurements reflecting size of braincase; largest member of the genus in external measurements on mainland Central America (larger congeners are distributed elsewhere in the Neotropics); upper incisors not noticeably procumbent, I2 equal to, or larger than, I1 in bulk; cingular shelf of P4 expanded posterolingually; parastyle and mesostyle of M1 reduced or absent; metastyle and metacrista of M1 elongate; mesostyle of M2 absent; lower incisors subtriangular in occlusal view, reduced in size, the inner incisor sometimes smaller than the outer, usually in pairs with a relatively large space between the left and right incisors and a smaller diastema between the teeth in each pair; premaxillae evenly rounded between canines and not noticeably elongate; pterygoid alae present; presphenoid ridge high and complete throughout; braincase domed, slope of rostrum relatively abrupt; mandibular symphyseal ridge well developed; pelage Cinnamon Brown to Olive Brown dorsally, Avellaneous to Drab ventrally; weight averaging 11.0 (9-15) in males and 11.4 (9-16) in nonparous females from throughout the range.

Comparisons

Characters by which *Glossophaga leachii* can be distinguished from *G. commissarisi* are in that account. Specimens of *Glossophaga leachii* are separated easily from those of *G. longirostris* by smaller size in measurements of cranial length and body weight, decumbent positioning of the upper incisors (noticeably procumbent in *G. longirostris*), reduced lower incisors that are paired with a larger gap between the left and right pairs (large and completely filling the space between the canines in *G. longirostris*), and in that the anterior border of the premaxillae is evenly rounded between the canines (noticeably elongate in *G. longirostris*). *G. leachii* also possesses well-developed pterygoid alae, a mandibular symphyseal ridge, and an expanded posterolingual cingular shelf of P4; each of these characters is usually absent in *G. longirostris*. These species are not sympatric.

Compared with *G. morenoi*, *G. leachii* has upper incisors that are not noticeably procumbent, the cingulum of P4 is expanded posterolingually, the mesostyle of M2 is absent, the anterior border of the premaxillae is evenly rounded between the canines, and the slope of the rostrum is relatively abrupt owing to the relatively massive braincase. In *G. morenoi*, as compared with *G. leachii*, the upper incisors are noticeably procumbent, P4 is narrow, the mesostyle of M2 is well developed, the anterior border of the premaxillae is elongate, and the slope of the braincase to rostrum is gradual. Specimens of *G. leachii* average larger than those of *G. morenoi* in external measurements and body weight; however, in measurements that reflect cranial length, particularly those of the rostrum and tooththrows, specimens of *G. morenoi* average larger than those of *G. leachii*. The presphenoid ridge, pterygoid alae, and mandibular symphyseal ridge are well developed in *G. leachii* but reduced or absent in *G. morenoi*.

Glossophaga leachii can be distinguished easily from *G. soricina* by the size and positioning of the incisors. In *G. leachii* the upper incisors are not noticeably procumbent and I2 is equal to, or larger than, I1 in bulk; the lower incisors are reduced in size, with noticeable gaps between the teeth. In *G. soricina*, the upper incisors are noticeably procumbent and I1 is much larger than I2 in bulk; the lower incisors are large and usually in contact. The anterior border of the premaxillae is evenly rounded between the canines in *G. leachii* (elongate in *G. soricina*), the parastyle and mesostyle of M1 are reduced or absent in *G. leachii* (well developed in *G. soricina*), and the mesostyle of M2 is absent in *G. leachii* (well developed in *G. soricina*). In areas where *G. leachii* is sympatric with *G. soricina*, specimens of the former average smaller than those of the latter in measurements of cranial length, but larger in measurements of cranial breadth and of the wing.

Ecology and Reproduction

Glossophaga leachii is known from the relatively xeric Pacific slopes in dry tropical, tropical deciduous, and pine-oak communities; marginal records barely extend into the more mesic tropical evergreen forests of the upper Caribbean versant. Specimens have been captured by hand or shot from daytime roosts (caves, buildings, and culverts); others have been collected in mist nets set across streams or in fields of cultivated plants.

Specimens of *G. leachii* have been collected at localities with *Saccopteryx bilineata*, *Noctilio leporinus*, *Pteronotus parnellii*, *Micronycteris megalotis*, *Lonchorhina aurita*, *Glossophaga commissarisi*, *G. morenoi*, *G. soricina*, *Carollia subrufa*, *Sturnira lilium*, *S. ludovici*, *Artibeus intermedius*, *A. jamaicensis*, *Dermanura phaeotis*, *Desmodus rotundus*, *Eptesicus furinalis*, and *Molossus* sp. in Chiapas (Webster, 1983), and *G. commissarisi* and *G. soricina* in Guatamala (Dickerman *et al.*, 1981). Davis and Russell (1952, 1954) took one *Choeronycteris mexicana* from the entrance of the same large, deep cave in Morelos that was occupied by many *Glossophaga leachii*, and Eguiarte *et al.* (1987) found *G. leachii*, *Leptoncycteris curasoeae*, and *Choeronycteris mexicana* foraging together on *Pseudobombax ellipticum* and *Ipomoea* sp. at 1950 meters in elevation at Tlayacapan, Morelos. Webb and Loomis (1977) reported on a trombiculid mite (*Hooperella vesperuginis*) that parasitizes *G. leachii*.

The reproductive condition of the 105 females (Table 8) examined by me does not clearly demonstrate any pattern of reproduction in *G. leachii*. It probably is similar to that of other congeners—that is, monotocous bimodal polyestry—but more data certainly are needed to substantiate this premise. Average length of testes, followed by sample size in parentheses, for males collected in the months from March to July are 4.0 (2), 3.5 (8), 4.0 (1), 2.0 (5), and 1.0 (1), respectively.

Geographic Variation

Univariate Analyses

Adult specimens from throughout the geographic range of *Glossophaga leachii* were grouped into seven samples (see Fig. 8) as follows: *sample 1*—COLIMA and JALISCO; *sample 2*—TLAXCALA, MORELOS, and GUERRERO; *sample 3*—VERACRUZ, OAXACA, and CHIAPAS; *sample 4*—GUATAMALA; *sample 5*—HONDURAS and EL SALVADOR; *sample 6*—NICARAGUA; *sample 7*—COSTA RICA. Standard statistics for all geographic samples are given in Table 9, and the results of four (length of third metacarpal, length of mandibular toothrow, breadth of braincase, and depth of braincase) SS-STP tests are given in Table 10.

External measurements.—Little can be said about geographic variation in external measurements of *G. leachii* inasmuch as a distinct pattern is not readily discernible. Specimens from southern Guatamala (4) and western México (1) average

TABLE 8.—*Recorded reproductive activity in females of Glossophaga leachii.*

Month	Number examined	Number pregnant	Number lactating
January	-	-	-
February	16	6	2
March	8	0	1
April	7	3	0
May	4	0	0
June	16	3	1
July	20	4	0
August	15	7	0
September	1	1	0
October	3	0	0
November	14	2	10
December	1	0	0

larger than those in all other samples in measurements of the wing, whereas specimens from southern México (3) average smaller. Males from Costa Rica (7) and females from western Nicaragua (6) also average smaller than those from other samples, but females from Costa Rica (7) are larger than average for other samples of that sex.

Cranial measurements.—Patterns of variation in measurements of cranial length (greatest length of skull, condylobasal length, length of rostrum, length of maxillary toothrow, length of mandibular toothrow, and mandibular length) are similar. Males and females from western Nicaragua (6), the male from Jalisco (1), and females from southern Guatamala (4) are smaller than average for the species in most measurements of cranial length, but specimens from other samples do not exhibit a distinct pattern of geographic variation. Males from southern Honduras and El Salvador (5) tend to be larger than males in other samples in some of the aforementioned measurements (greatest length of skull, condylobasal length, and mandibular length), and males from Costa Rica (7) average larger than males from other samples in length of maxillary and mandibular toothrows. Females from Tlaxcala, Morelos, and Guerrero (2) are larger than those from all other samples of females in length of maxillary toothrow, length of mandibular toothrow, and mandibular length. The two females from Colima (1) average larger than females in other samples in greatest length of skull and condylobasal length, and together with females from Costa Rica (7) average larger than those in other samples in length of rostrum.

Males from samples 4-5 (Guatamala, Honduras, and El Salvador) average larger than males in other samples in most measurements reflecting width and depth of the cranium (zygomatic breadth, mastoid breadth, interorbital breadth, breadth of braincase, and depth of braincase). Females from Guatamala, Honduras, El Sal-

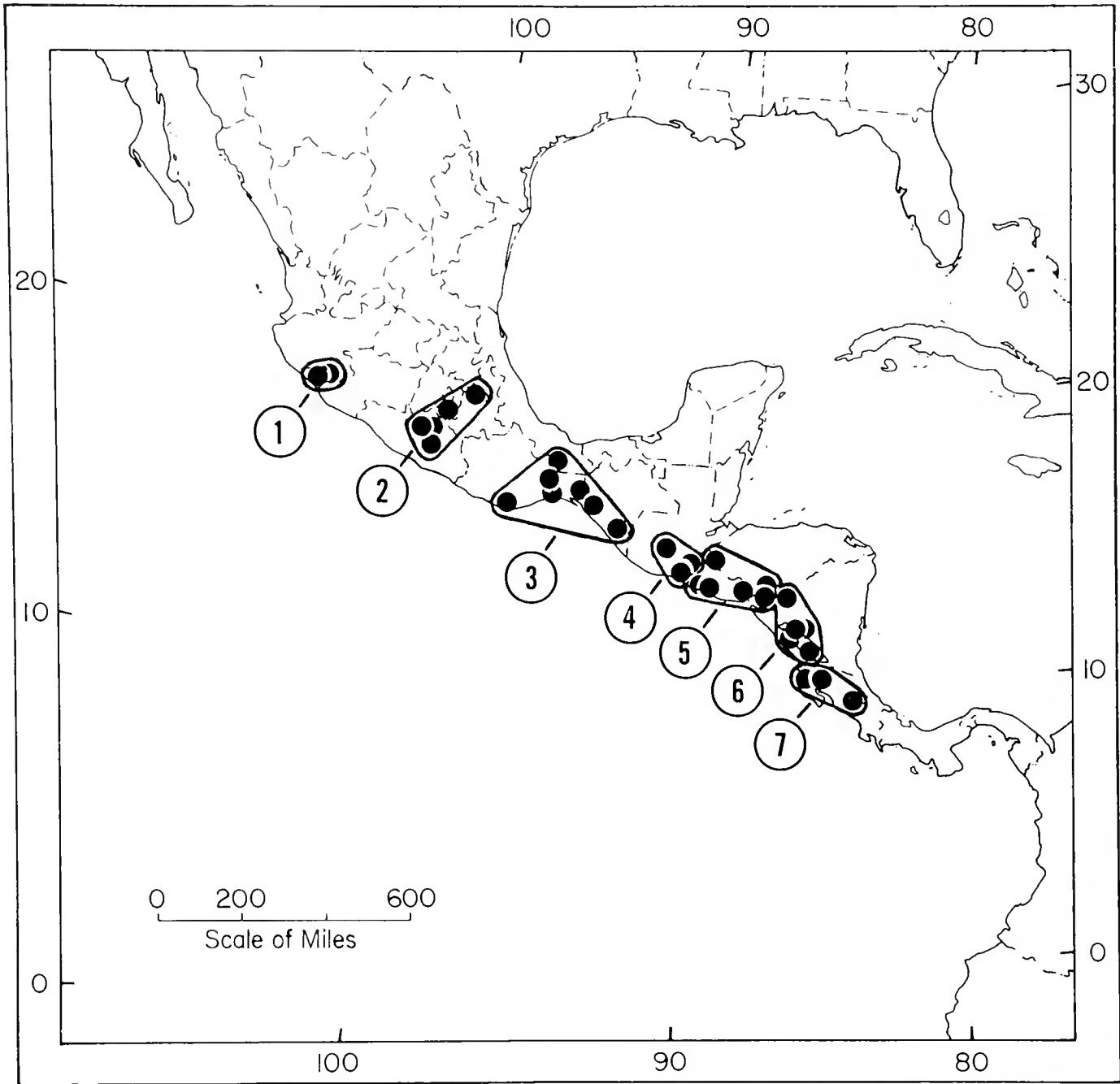


FIG. 8.—Approximate geographic areas included in the seven samples of *Glossophaga leachii* analyzed. See text for localities included in each sample.

vador, and Costa Rica (4-5, 7) average larger than females from other samples in breadth and depth of braincase, whereas those from western and southern México (1,3) average larger than females from other samples in the remaining measurements of cranial width. Conversely, the one male from Jalisco (1) examined is smaller than males from other samples in mastoid breadth, breadth of braincase, depth of braincase, and together with males from Costa Rica (7), averages smaller than other males in zygomatic breadth. Males from sample 6 (western Nicaragua) and sample 2 (Tlaxcala, Morelos, and Guerrero) average smaller than other samples of males in interorbital breadth. Females from central México (2) and western Nicaragua (6) average smaller than females from other samples in most measurements of cranial width and depth.

TABLE 9.—*Geographic variation in external and cranial measurements among seven samples of Glossophaga leachii. See text and Figure 8 for key to sample numbers.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of forearm</i>								
1	1	36.80			2	37.00	36.3–37.7	1.98
2	26	36.51	33.5–38.1	2.13	15	37.07	36.7–38.2	1.61
3	13	36.11	34.7–37.4	1.50	17	36.53	34.5–37.8	1.72
4	4	36.73	36.5–36.9	0.34	1	37.40		
5	10	36.77	35.4–38.1	1.97	11	36.83	35.9–37.4	1.10
6	10	36.31	35.3–36.9	1.13	6	37.00	35.7–38.6	2.25
7	4	36.25	35.0–38.5	3.17	4	37.63	37.0–38.2	1.01
<i>Length of third metacarpal</i>								
1	1	38.20			2	37.15	36.6–37.7	1.56
2	26	36.46	33.6–39.0	2.54	15	36.43	33.3–38.2	2.44
3	13	36.01	34.4–37.1	1.74	17	36.34	33.7–38.2	2.24
4	8	36.86	36.2–38.2	1.15	3	36.90	36.4–37.5	1.11
5	10	36.64	35.2–37.6	1.34	11	36.53	34.8–37.7	1.71
6	10	36.67	35.2–38.8	2.08	6	36.30	35.0–37.6	1.93
7	4	35.90	35.3–36.8	1.40	4	36.88	36.0–38.3	2.09
<i>Length of fourth metacarpal</i>								
1	1	34.60			2	34.50	34.3–34.7	0.57
2	27	33.87	31.1–35.7	2.28	15	33.98	30.9–36.3	2.53
3	13	33.11	32.0–34.8	2.00	17	33.57	31.5–35.5	2.22
4	8	34.15	32.9–35.3	1.47	3	34.03	33.5–34.9	1.51
5	10	33.75	32.2–34.8	1.80	11	33.90	33.0–35.0	1.41
6	10	33.71	31.7–35.8	2.42	6	33.42	32.6–34.2	1.36
7	4	33.05	32.1–34.3	2.25	4	34.40	33.1–36.0	2.56
<i>Length of fifth metacarpal</i>								
1	1	33.60			2	32.50	32.2–32.8	0.85
2	27	32.50	29.7–34.3	2.09	15	32.72	29.9–34.4	2.47
3	13	32.22	30.8–34.8	2.04	17	32.58	30.7–34.5	2.06
4	8	32.89	32.3–34.0	1.30	3	32.93	32.3–33.7	1.42
5	10	32.67	31.5–33.6	1.47	11	33.11	32.3–34.1	1.09
6	10	32.61	31.0–34.0	1.82	6	32.30	30.2–33.2	2.23
7	4	31.73	30.9–32.7	1.50	4	33.23	32.4–34.5	1.91
<i>Greatest length of skull</i>								
1	1	20.30			2	20.80	20.6–21.0	0.57
2	27	20.49	20.0–21.0	0.60	14	20.74	20.0–21.7	0.95
3	12	20.65	19.8–21.5	1.04	18	20.78	20.0–21.4	0.73
4	5	20.68	20.1–21.3	0.92	1	20.50		
5	10	20.70	20.3–21.2	0.59	11	20.69	20.2–21.4	0.67
6	10	20.22	19.8–20.7	0.66	6	20.52	19.9–21.0	0.98
7	4	20.38	19.8–20.8	0.84	4	20.75	20.3–21.0	0.66

TABLE 9.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Condylobasal length</i>								
1	1	18.60			2	19.20	19.1–19.3	0.28
2	27	18.96	17.8–19.5	0.77	14	19.19	18.1–20.4	1.07
3	3	18.96	18.4–19.9	0.96	18	19.14	18.4–19.6	0.72
4	7	18.96	18.7–19.5	0.54	3	18.80	18.6–19.0	0.40
5	10	19.08	18.7–19.6	0.56	11	18.98	18.6–19.6	0.59
6	10	18.61	18.1–19.0	0.59	6	18.85	18.4–19.2	0.72
7	4	18.83	18.6–19.0	0.34	4	19.08	18.7–19.5	0.70
<i>Zygomatic breadth</i>								
1	1	9.30			2	9.65	9.6–9.7	0.14
2	24	9.50	9.1–9.9	0.40	10	9.43	8.9–9.8	0.51
3	9	9.53	9.0–10.0	0.55	15	9.65	9.2–10.0	0.45
4	4	9.64	9.3–9.9	0.48	2	9.60	9.5–9.7	0.28
5	8	9.68	9.4–10.0	0.38	11	9.57	9.1–9.8	0.39
6	9	9.49	9.3–9.7	0.23	5	9.50	9.2–9.7	0.40
7	3	9.30	9.2–9.4	0.20	4	9.50	9.3–9.9	0.54
<i>Length of rostrum</i>								
1	1	7.70			2	8.15	8.0–8.3	0.42
2	29	8.10	7.5–8.6	0.45	15	8.14	7.6–8.6	0.45
3	12	8.13	7.9–8.5	0.38	18	8.13	7.9–8.5	0.38
4	7	8.03	7.9–8.3	0.28	3	7.97	7.9–8.1	0.23
5	10	8.09	7.9–8.3	0.29	11	8.08	7.7–8.4	0.37
6	10	7.87	7.5–8.2	0.40	6	7.98	7.6–8.3	0.56
7	4	8.10	7.8–8.2	0.40	4	8.15	7.9–8.4	0.42
<i>Mastoid breadth</i>								
1	1	9.00			2	9.20	9.2	0.00
2	24	9.11	8.9–9.4	0.29	12	9.03	8.7–9.5	0.47
3	13	9.13	8.6–9.6	0.56	18	9.16	8.9–9.7	0.41
4	7	9.16	9.0–9.3	0.23	3	9.17	8.9–9.3	0.46
5	10	9.31	9.1–9.6	0.42	11	9.15	8.8–9.4	0.35
6	10	9.12	8.8–9.5	0.43	6	8.98	8.7–9.2	0.39
7	4	9.23	9.1–9.3	0.19	4	9.23	8.9–9.4	0.44
<i>Interorbital breadth</i>								
1	1	4.10			2	4.25	4.2–4.3	0.14
2	27	3.98	3.7–4.2	0.26	15	4.03	3.7–4.3	0.34
3	12	4.06	3.8–4.3	0.29	18	4.18	4.0–4.4	0.23
4	7	4.13	4.0–4.3	0.19	3	4.00	3.8–4.3	0.53
5	10	4.14	3.9–4.3	0.23	11	4.14	4.0–4.4	0.30
6	10	3.98	3.8–4.2	0.26	5	4.08	3.9–4.2	0.26
7	4	4.05	3.9–4.2	0.26	4	4.03	3.9–4.2	0.25

TABLE 9.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Breadth of braincase</i>								
1	1	8.50			2	8.70	8.7	0.00
2	25	8.66	8.4–9.0	0.34	13	8.65	8.3–8.9	0.37
3	13	8.63	8.2–8.9	0.45	18	8.72	8.4–9.0	0.37
4	7	8.74	8.6–8.9	0.23	3	8.80	8.4–9.1	0.72
5	10	8.74	8.5–9.0	0.34	11	8.85	8.7–9.2	0.29
6	10	8.67	8.4–9.0	0.41	6	8.62	8.2–8.9	0.50
7	4	8.68	8.6–8.8	0.19	4	8.80	8.7–9.0	0.28
<i>Depth of braincase</i>								
1	1	7.00			2	7.10	7.0–7.2	0.28
2	26	7.07	6.0–7.4	0.52	14	7.06	6.6–7.5	0.53
3	13	7.12	6.8–7.4	0.38	18	7.18	6.8–7.6	0.45
4	7	7.20	7.0–7.3	0.23	3	7.33	7.1–7.6	0.50
5	10	7.24	6.9–7.5	0.40	11	7.27	7.0–7.6	0.40
6	9	7.17	6.9–7.3	0.33	6	7.12	6.9–7.3	0.34
7	4	7.18	7.1–7.2	0.10	4	7.23	6.9–7.4	0.44
<i>Length of maxillary toothrow</i>								
1	1	6.80			2	7.05	7.0–7.1	0.14
2	28	7.02	6.6–7.3	0.39	15	7.13	6.6–7.3	0.36
3	13	7.02	6.7–7.3	0.37	18	7.08	6.8–7.3	0.33
4	7	7.00	6.7–7.2	0.33	1	7.10		
5	10	7.01	6.9–7.1	0.18	10	7.04	6.8–7.3	0.29
6	10	6.91	6.7–7.2	0.32	6	6.98	6.7–7.2	0.39
7	4	7.08	6.8–7.2	0.38	4	6.98	6.7–7.1	0.38
<i>Length of mandibular toothrow</i>								
1	1	7.40			2	7.40	7.3–7.5	0.28
2	28	7.43	7.0–7.9	0.41	14	7.46	7.3–7.7	0.23
3	13	7.44	7.0–7.9	0.49	18	7.44	7.2–7.8	0.35
4	4	7.48	7.3–7.7	0.34	1	7.40		
5	10	7.36	7.2–7.6	0.29	11	7.36	7.2–7.5	0.22
6	9	7.32	7.0–7.6	0.37	6	7.35	7.1–7.5	0.33
7	4	7.50	7.1–7.7	0.57	4	7.40	7.1–7.7	0.40
<i>Width across molars</i>								
1	1	5.40			2	5.65	5.5–5.8	0.42
2	26	5.68	5.4–6.0	0.31	15	5.75	5.3–6.1	0.39
3	11	5.61	5.4–5.8	0.29	18	5.67	5.4–5.9	0.28
4	7	5.53	5.3–5.8	0.41	2	5.60	5.5–5.7	0.28
5	9	5.63	5.5–5.7	0.14	9	5.64	5.5–5.8	0.25
6	10	5.54	5.3–5.8	0.33	6	5.65	5.3–5.8	0.35
7	4	5.58	5.5–5.7	0.19	4	5.50	5.4–5.6	0.16

TABLE 9.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
Mandibular length								
1	1	13.00			2	13.45	13.3–13.6	0.42
2	27	13.30	12.7–14.1	0.60	13	13.55	13.2–14.2	0.60
3	13	13.19	12.6–13.7	0.65	18	13.42	12.9–14.1	0.71
4	6	13.28	13.0–13.7	0.59	3	13.23	13.2–13.3	0.12
5	9	13.42	13.2–13.8	0.41	10	13.37	12.9–13.8	0.57
6	10	13.04	12.6–13.4	0.50	5	13.20	12.7–13.5	0.60
7	4	13.15	12.8–13.4	0.60	4	13.53	13.1–13.8	0.62

Width across molars exhibits a different pattern of geographic variation. Specimens from Tlaxcala, Morelos, and Guerrero (2) average broader than those from all other samples in width across molars, yet females from the same sample are extremely narrow in other measurements of cranial width as noted in the preceding paragraph. Females from sample 7 (Costa Rica) and the male from Jalisco (1) average smaller than specimens in all other samples in width across molars.

Pelage coloration.—There is some degree of clinal variation in pelage coloration in that specimens from Costa Rica (7) and western Nicaragua (6) average darker than average, whereas those to the northern part of the geographic range for the species average paler. Bats from southern Guatamala (4), however, are darker than those from samples to the immediate northwest and southeast. Color was not assessed in the male from Jalisco (1) because the skin is preserved in fluid, but females from this sample average paler than bats in all other samples.

Qualitative cranial characters (Table 5).—In *Glossophaga leachii*, pterygoid alae are well (72.1 percent) or modestly developed (20.9 percent); they were lacking in only nine of 129 (7.0 percent) individuals examined. Specimens from southern Guatamala (4) most frequently lack pterygoid alae, whereas those from Colima and Jalisco (1) and Costa Rica (7) always have alae that are moderately to well developed.

The presphenoid ridge is almost always (98.5 percent) continuous and high throughout in *G. leachii*. Only two of 130 (1.5 percent) specimens, a female from Morelos and another from Honduras, have a ridge that is only moderately prominent. No individuals possess an incomplete presphenoid ridge.

The upper incisors are not noticeably procumbent (73.4 percent), or only modestly so (23.4 percent), in *G. leachii*; specimens from samples 5-7 (El Salvador, Honduras, Nicaragua, and Costa Rica) have the highest incidence of upper incisors that are not noticeably procumbent. The angle of projection of the upper incisors is noticeably procumbent in only four of 124 (3.2 percent) individuals, those being a male and two females from Oaxaca and a male from Guerrero.

TABLE 10.—Results of four SS-STP tests of geographic variation in *Glossophaga leachii*. Vertical lines to the right of sample means connect maximally nonsignificant subsets at the 0.05 probability level for length of third metacarpal, length of mandibular toothrow, breadth of braincase, and depth of braincase. See text and Figure 8 for key to samples.

Sample number	Males		Sample number	Female	
	Mean	Results SS-STP		Mean	Results SS-STP
<i>Length of third metacarpal</i>					
1	38.20		2	37.15	
4	36.86		4	36.90	
6	36.67		7	36.88	
5	36.64		5	36.53	
2	36.46		2	36.43	
3	36.01		3	36.34	
7	35.90		6	36.30	
<i>Length of mandibular toothrow</i>					
7	7.50		2	7.46	
4	7.48		3	7.44	
3	7.44		4	7.40	
2	7.43		1	7.40	
1	7.40		7	7.40	
5	7.36		5	7.36	
6	7.32		6	7.35	
<i>Breadth of braincase</i>					
4	8.74		5	8.85	
5	8.74		7	8.80	
7	8.68		4	8.80	
6	8.67		3	8.72	
2	8.66		1	8.70	
3	8.63		2	8.65	
1	8.50		6	8.62	
<i>Depth of braincase</i>					
5	7.24		4	7.33	
4	7.20		5	7.27	
7	7.18		7	7.23	
6	7.17		3	7.18	
3	7.12		6	7.12	
2	7.07		1	7.10	
1	7.00		2	7.06	

The upper incisors in *G. leachii* are equal (43.9 percent) or subequal (25.2 percent) in bulk. The upper incisors were unequal in bulk, the outer pair the larger, in 30.9 percent of the specimens examined by me; and as described in the account of *G. commissarisi*, this bimodality results from the three character states not being continuous. Specimens of *G. leachii* from southern Guatamala (4) and Costa Rica (7) tend to have upper incisors that are equal in bulk, but the two females from Colima (1) have unequal upper incisors, the outer pair being conspicuously larger than the inner.

Lower incisors are usually medium in size but not in contact (80.2 percent) in *G. leachii*. In some specimens, the lower incisors are small and evenly spaced (2.5 percent) or small and paired (4.1 percent); in others they are large and in contact (13.2 percent), especially those in specimens from Guerrero and Morelos (2) where the incidence of large lower incisors is highest. This character tends to be more variable overall in bats from central and southern México than in other parts of the range of *G. leachii*.

The upper premolars are usually unequal in bulk (89.2 percent) in *G. leachii*, the larger P4 possessing a conspicuous posterolingual cingulum that is lacking on P3. Upper premolars were subequal in bulk in 9.2 percent of the individuals examined; equal-sized premolars were present in only two of 130 (1.5 percent) specimens, a female from Guatamala and another from El Salvador.

In *G. leachii*, there is a subtle north to south cline in the depth of the basisphenoid pits, resulting in shallower pits in specimens from central and southern México (2-3) and deeper pits in those from the southern part of the range of the species. Overall, however, the basisphenoid pits are moderately deep (68.2 percent) in members of this species. The majority of the 16 individuals (of 129, 12.4 percent) with shallow pits are from Guerrero, Morelos, Oaxaca, and southern Guatamala (2-4), whereas most of the 25 specimens (19.4 percent) with deep basisphenoid pits are from El Salvador, Nicaragua, and Costa Rica (5-7). Specimens from samples 3-4 (southern México and Guatamala) are the most variable in this character.

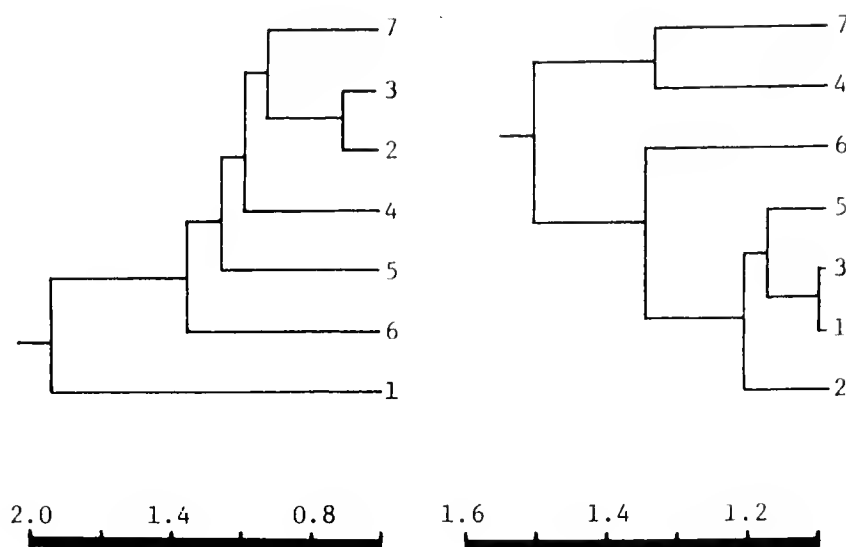
The rostral slope usually is moderate (57.3 percent) in *G. leachii*, never being continuous from rostrum to braincase as in other congeners. Of the specimens with a gradual slope (22.1 percent), most are from El Salvador, Honduras, and Nicaragua (5-6), whereas the majority of individuals with an abrupt slope (20.6 percent) are from central and southern México and southern Guatamala (2-4).

Posterior palatine processes were poorly developed in 48.1 percent of the specimens of *G. leachii* examined by me. They are better developed in specimens from Guerrero than in those from Morelos, hence the high variability associated with specimens from sample 2. Processes were greatly or moderately developed in 17.6 and 22.1 percent, respectively, of the specimens of *G. leachii* studied, the remaining 12.2 percent of the specimens lacked posterior palatine processes all together. Overall, there seems to be little pattern to geographic variation in this character.

Multivariate Analysis

The 26 characters (16 quantitative, color, and nine qualitative) were analyzed with the NT-SYS program; phenetic relationships of male and female *G. leachii* were displayed using phenograms that were computed on correlation and distance matrices. Distance phenograms are figured herein because they have larger coeffi-

FIG. 9.—Distance phenograms for seven samples of *Glossophaga leachii*. Phenograms were computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages for males (left) and females (right). The cophenetic coefficient of correlation for the phenogram for males is 0.933 and for females is 0.697. See Figure 8 and text for key to samples.



cients of cophenetic correlation (Fig. 9). Distance coefficients between adjacent samples for each sex are shown in Fig. 10.

Male *G. leachii* loosely cluster into one unit in the distance phenogram. Males from central and southern México (2-3) form a distinct phenetic unit within this large cluster because they average larger than males in other samples in measurements of cranial length, smaller than those in other samples in cranial width, and because they possess relatively shallow basisphenoid pits. All other samples of males fit well within this large cluster except the one male from Jalisco (1), which is much larger than average for males in wing measurements, but much smaller in most cranial dimensions.

The distance phenogram for females indicates that the samples cluster into three distinct groups. Specimens from southern Guatamala (4) and Costa Rica (7) form a unit that is characterized by large external size, a large braincase, narrow space between the orbits, deep basisphenoid pits, and upper incisors that are equal in bulk. Females from México (1-3), southern Honduras and El Salvador (5) constitute another phenetically distinct group; specimens from these samples tend to have shallow basisphenoid pits and average larger in measurements of cranial length than do other females. Those from sample 6 (western Nicaragua) comprise the third group in the distance phenogram. Specimens from western Nicaragua are smaller than females in other samples in measurements of the wing and cranium, and the slope from rostrum to braincase is more gradual because the braincase is much less inflated.

The first four principal components combine to express 89.6 percent of the phenetic variation in males and 85.4 percent in females. The amount of variation expressed in the first four principal components for males and females, respectively, was 50.5 and 35.8 for component I, 17.1 and 23.3 for component II, 14.1 and 13.8 for component III, and 7.9 and 12.5 for component IV. Characters with loadings above 0.60 (or below -0.60) on any of the first four principal components are

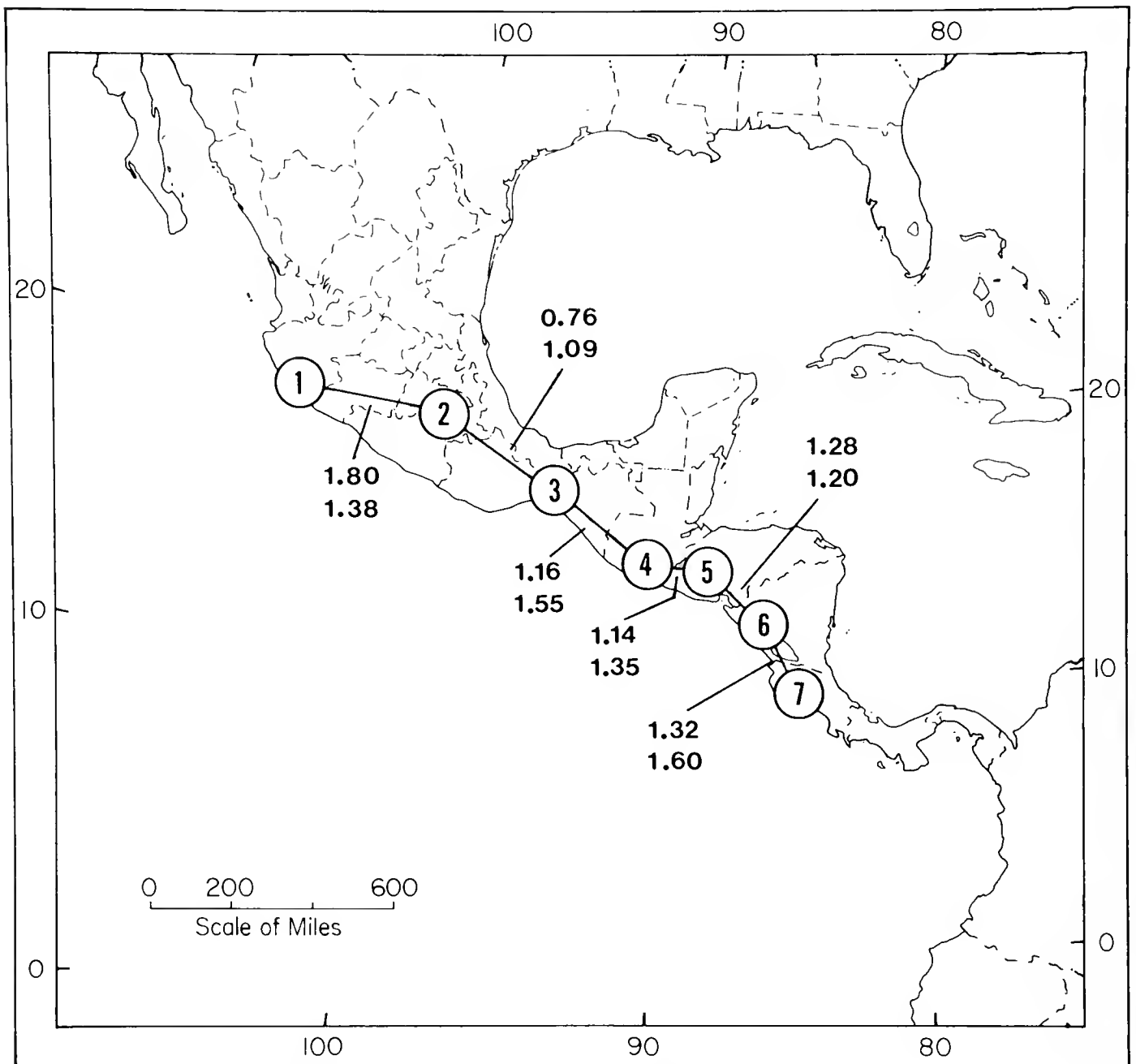


FIG. 10.—Selected distance coefficients between adjacent samples of *Glossophaga leachii*. Coefficients are from distance matrices for males (above) and females (below). See Figure 8 and text for key to samples.

shown in Table 11. Two-dimensional plots of principal components I-II are shown for both sexes (Fig. 11).

The two-dimensional plots of male and female *G. leachii* demonstrate the same cluster patterns as in the distance phenograms. For samples of males, only one OTU, the single male from Jalisco (1), is divergent on both component I and II; this specimen is large externally but small cranially. OTUs on the left-hand side of component I average smaller in external measurements, and those to the bottom of component II are larger than average in cranial dimensions. In the plot of female samples, OTUs to the right-hand side of component I are smaller than average in measurements of cranial length and most often lack pterygoid alae. Component II best reflects the clusters from the distance phenogram for female samples. OTUs to the bottom (4,7) of this component are large in measurements of the wing, have a more inflated braincase, more abrupt rostral slope, and deeper basisphenoid pits;

TABLE 11.—*Factor loadings for 26 characters examined in Glossophaga leachii. Only loadings above 0.600 (or below -0.600) on the first four principal components are shown (males above, females below).*

Character	I	II	III	IV
Length of forearm	0.939			
Length of third metacarpal	0.883	-0.752		
Length of fourth metacarpal	0.892	-0.670		
Length of fifth metacarpal	0.884	-0.647		
Greatest length of skull	-0.912	-0.848		
Condylobasal length	-0.920	-0.881		
Zygomatic breadth		-0.917		-0.805
Length of rostrum	-0.621 -0.968	-0.681		
Mastoid breadth		-0.760		
Interorbital breadth	0.670		-0.869	
Breadth of braincase		-0.865 -0.741		-0.894
Depth of braincase		-0.753 -0.669		
Length of maxillary toothrow	-0.634		-0.969	
Length of mandibular toothrow			-0.927 -0.718	
Width across molars	-0.624	-0.632 0.602		
Mandibular length	-0.949		-0.736	
Pelage coloration	-0.666	-0.627		
Pterygoid alae				0.871 -0.610
Presphenoid ridge	-0.889			
Lower incisors			-0.713 -0.755	
Upper incisor angle		-0.620		
Upper incisor size		-0.651		0.752

TABLE 11.—Continued.

Character	I	II	III	IV
Basisphenoid				−0.847
pits		−0.649		
P3:P4			−0.926	
bulk	0.667	−0.675		
Rostral slope			−0.952	
		−0.841		
Postpalatal	−0.697	−0.657		
processes				−0.787

the one at the top (6) is comprised of bats that are small externally and that have a gradual rostral slope leading to a relatively small braincase, whereas those in the middle (1-3, 5) compromise these characters in various combinations.

Taxonomic Conclusions

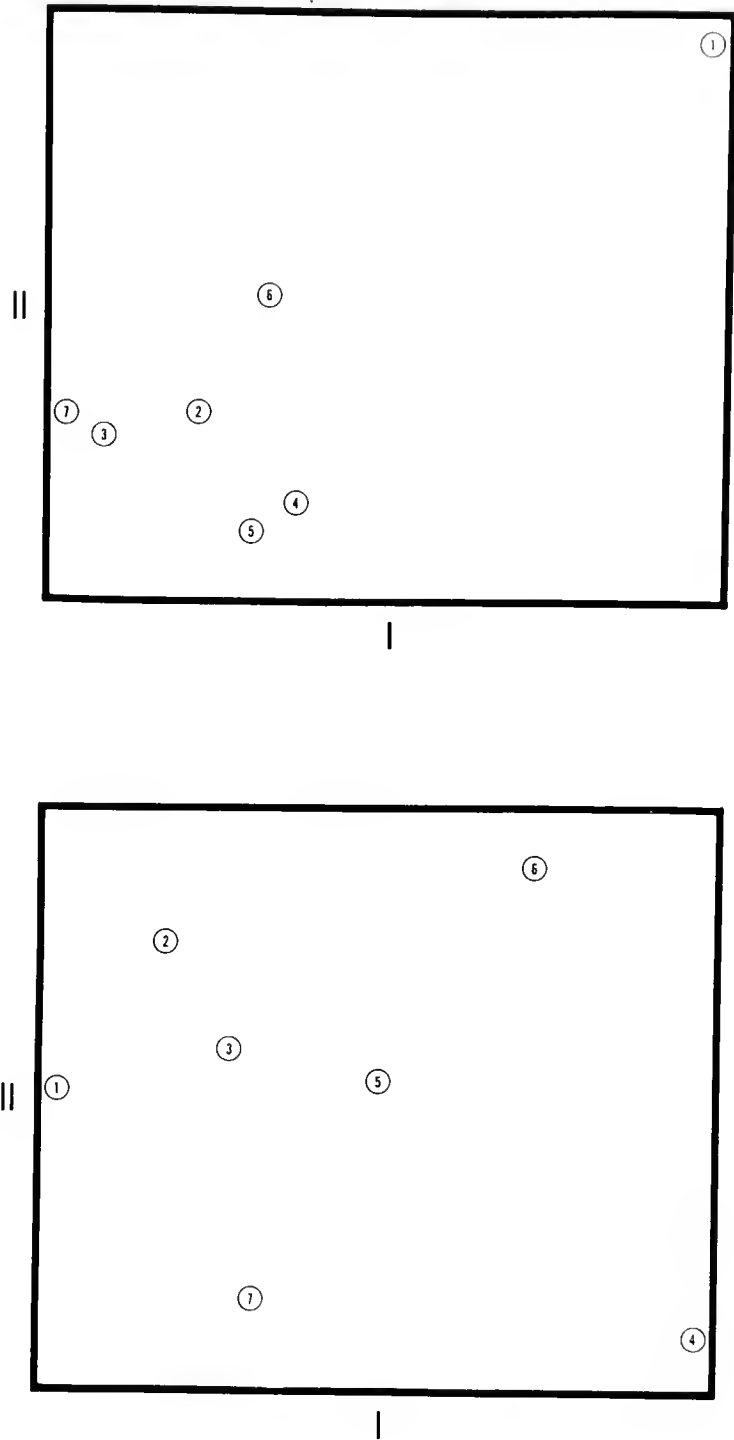
In that no pattern of geographic variation indicates a zone of reduced gene flow, the population of bats to which the binomial *Glossophaga leachii* (Gray) applies is considered to be monotypic throughout its geographic range from west-central México (Colima, Jalisco, and Tlaxcala) southeastward to central Costa Rica. Specimens from Nicaragua tend to be smaller than average for the species in most external and cranial measurements. Clinal variation is evident in at least two characters, with individuals from the south averaging darker in pelage color and possessing deeper basisphenoid pits than specimens from farther north. The distinct nature of individuals from western México, particularly males, is an artifact of sample size, a problem that surely will be remedied with the acquisition of more specimens from this part of the range of the species.

Glossophaga leachii (Gray)

1844. *Monophyllus leachii* Gray, Mammalia, in The zoology of the voyage of H.M.S. Sulphur . . . , 1:18, April.
1847. *N[icon]. caudifer* Gray, Proc. Zool. Soc. London, p.15, 13 April; “renaming of *leachii* wrongly supposed to be identical with the *Glossophaga caudifer* of Geoffroy” (see Miller, 1913b:419).
1944. *Glossophaga soricina alticola* Davis, J. Mamm., 25:377, 12 December; holotype from 13 km. NE Tlaxcala, 7800 ft., Tlaxcala, México.
1980. *Glossophaga leachii*, Webster and Jones, Occas. Papers Mus., Texas Tech Univ., 71:4, 7 November.

Holotype.—Adult of undetermined sex, British Museum (of Natural History) 42.8.17.17, from Realejo, Chinandega, Nicaragua; obtained by J. Gould on an unspecified date. Holotype examined by J. K. Jones, Jr., D. C. Carter, and C. O. Hand-

FIG. 11.—Two-dimensional plots for seven samples of *Glossophaga leachii*. Component I plotted against component II for males (top) and females (bottom). See Figure 8 and text for key to samples.



ley, Jr., their notes made available to me in unpublished form; photographs of cranium and lower jaw, provided by A. L. Gardner, are in Webster and Jones (1980:3). Skin and skull in poor condition, most of occipital and basioccipital region of cranium missing (Carter and Dolan, 1978); pterygoid and palatal regions essentially undamaged, upper and lower teeth intact (Webster and Jones, 1980).

Measurements of the holotype.—Selected external and cranial measurements from Carter and Dolan (1978) are: length of forearm (dry), 36.4; length of maxillary toothrow, 6.7.

Distribution.—This monotypic species is known from central México (Colima, Jalisco, and Tlaxcala) southeastward to central Costa Rica (Fig. 12); known altitudinal distribution from near sea level to at least 2380 meters in elevation.

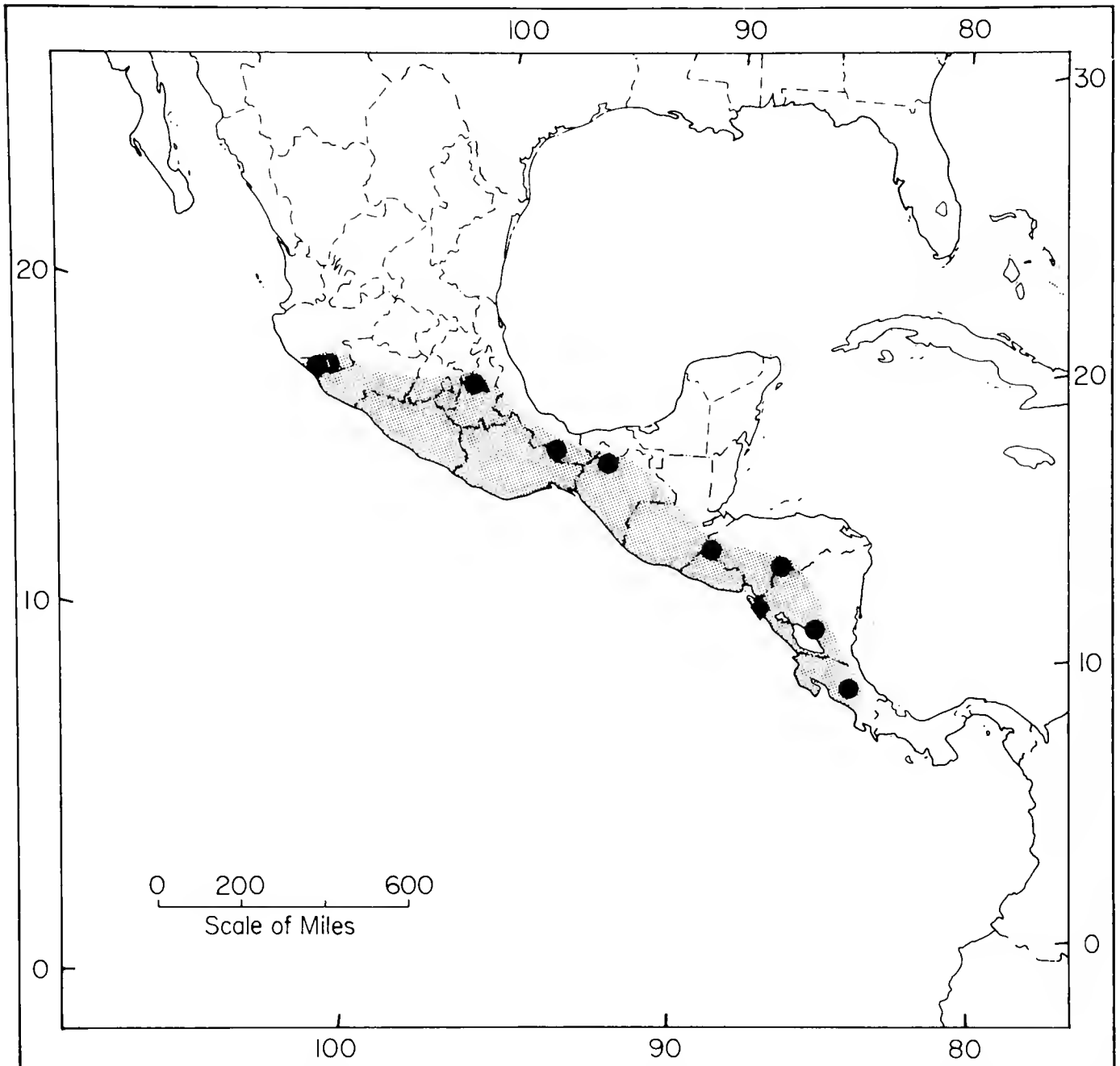


FIG. 12.—Geographic distribution of *Glossophaga leachii*. Circles represent marginal localities and the diamond represents the type locality.

Comparisons.—*Glossophaga leachii* most closely resembles *G. commissarisi* in cranial dimensions and dental morphology, but *G. leachii* possesses well-developed pterygoid alae and a presphenoid ridge, whereas *G. commissarisi* lacks both of these structures. The upper incisors of *G. longirostris*, *G. morenoi*, and *G. soricina* are noticeably procumbent, whereas those of *G. leachii* tend to be less procumbent.

Remarks.—The taxonomic history of *G. leachii* has been a confusing one. Webster and Jones (1980) concluded that *Monophyllus leachii* Gray, 1844, represents what was previously known as *Glossophaga alticola* Davis, 1944; furthermore, they synonymized *Glossophaga morenoi* Martínez and Villa-R., 1938, with *G. leachii* following Villa-R. (1953, 1964, 1967). Gardner (1986), however, acting on information subsequently provided by Webster and Jones (1984a), allocated the name *G. morenoi* to the species of bat named and described by Webster and Jones (1980).

as *G. mexicana*, thereby removing *G. morenoi* from the taxonomic synonymy of *G. leachii*, a situation that is discussed in more detail in the account of *G. morenoi*.

Average external measurements (extremes in parentheses) of 70 males, followed by those of 52 females, of *G. leachii* are: total length, 63.7 (50-72), 63.9 (55-72); length of tail, 6.2 (1-11 in 57 specimens), 7.0 (2-11 in 47 specimens); length of hind foot, 10.3 (5-13), 10.4 (8-12); length of ear from notch, 13.3 (7-16), 13.5 (8-16).

Specimens examined (338).—COSTA RICA. *Alajuela*: Grecia, 3600 ft., 18 (AMNH). *Cartago*: Tres Rios, 4000 ft., 4 (AMNH). *Guanacaste*: 1 km. SSE Bagaces, 75 m., 2 (KU); 0.5 mi. E Finca Jiménez, 30 m., 2 (UMMZ); Finca la Pacífica, Río Tenorito, 1 (UMMZ); Playa del Cocos, sea level, 3 (2 MVZ, 1 LSU). *San José*: San Isidro, 4733 ft., 2 (AMNH); San José, 3800 ft., 1 (LSU). *No locality*: 1 (AMNH). EL SALVADOR. *Cuscatlán*: Suchitoto, 380 m., 1 (TCWC). *La Libertad*: 0-3.5 km. W La Libertad, 10-15 m., 3 (TCWC); 5.1 km. E La Libertad, 2 (TCWC); 16.8 km. W La Libertad, 30 m., 2 (TCWC). *La Unión*: Río Goascorán, 150 m., 2 (MVZ). *Sonsonate*: 31 km. W La Libertad, sea level, 1 (TCWC). GUATAMALA. *Chiquimula*: 20 km. SSE Chiquimula, 550 m., 4 (TCWC). *El Progreso*: El Progreso, 6 (AMNH). *Jutiapa*: 7 mi. S Ascunción Mita, 2 (FMNH); Jutiapa, 14 (FMNH); 2.5 mi. W, 2.25 mi. N San Cristóbal Frontera, 2900 ft., 3 (KU). *Santa Rosa*: Chiquimulilla, 1 (USNM). *Sololá*: San Lucas, 1 (AMNH). HONDURAS. *Choluteca*: Choluteca, 5 (CMNH); 36 km. SE Choluteca, 600 m., 1 (TCWC). *Comayagua*: ca. Comayagua, 10 (TCWC). *El Paraíso*: Chichicaste, 480 m., 1 (TCWC); 3 mi. S Güinope, 1 (TCWC). *Francisco Morazán*: 2 mi. S La Venta, 420 m., 4 (TCWC); Tegucigalpa (Cuestra lempira), 1 (CMNH); El Zamorano, 1 (TCWC). *Ocatepeque*: 4 km. N Nueva Ocatepeque, 840 m., 6 (TCWC). *Valle*: 6 km. E Amatillo, 60 m., 2 (TCWC); 10 km. E San Lorenzo, 25 ft., 1 (TCWC). MEXICO. *Chiapas*: Acala, 13.5 mi. SW San Cristóbal de las Casas, ca. 3000 ft., 1 (TCWC); 5-6 km. N Arriga, 600-800 ft., 5 (TCWC); 4 mi. NE Chiapa de Corzo, 3000 ft., 1 (TCWC); 32 mi. SW Cintalapa, 8 (TTU); 42 km. W Cintalapa, Rancho San Fernando, ca. 2000 ft., 1 (UA); 23.6 mi. NW Huixtla, 400 ft., 1 (TCWC); 17 mi. W, 4 mi. S Las Cruces, ca. 2000 ft., 2 (KU); 7 km. WNW Mal Paso, 1 (TCWC); 10-12 mi. W Mal Paso, 2 (TCWC); 5 km. ESE Pichucalco, 200 ft., 2 (TCWC); Puente Vado Ancho, km. 184 on Hwy. 200, ca. 17 km. NW Huixtla, 1 (UA); Río Dorado, 40 km. SSE Tuxtla Gutiérrez, 1800 ft., 19 (TCWC); 8 km. S Solusuchiapa, ca. 400 ft., 2 (UA); 8 mi. SE Tonalá, Finca Ocuilapa, ca. 100 ft., 1 (LACM); 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa, 17 (TTU); 9 mi. SE (and then) 8 mi. NE Tonalá, 7 (LACM); 15 mi. ESE Tonalá, 1 (LACM). *Colima*: Comala, 2 (LACM). *Guerrero*: Acahuizotla, 2800 ft., 1 (TCWC); 1.9 km. W El Carrizal, Hwy. 200, 2 (TTU); km. 121 from México City to Acapulco, Hwy. 95, 1 (UA); km. 157 from México City to Acapulco, Hwy. 95, 2 (UA); km. 231 from México City to Acapulco, Hwy. 95, 1 (UA); 1 mi. SE San Andrés de la Cruz, 700 m., 5 (UMMZ); 4 km. NW Teloloapan, Alpíaxia, 1540 m., 1 (KU); 8 mi. N, 1 mi. W Teloloapan, 3600 ft., 33 (KU); 1.5 mi. SSW Yerbabuena, Cueva de tia Juana, 1840 m., 13 (KU). *Jalisco*: 10 mi. NNE Pihuamo, 3500 ft., 1 (KU). *Morelos*: Cuernavaca, 2 (USNM); 3 km. E Jonacatepec, 4500 ft., 10 (TCWC); Oaxtepec, 1 (USNM); Santa Clara, 3500 ft., 4 (TCWC). *Oaxaca*: Chicapa, 100 ft., 1 (USNM); 20 mi. NE La Ventosa, 6 (AMNH); 34 mi. (by Hwy. 190) La Ventosa Jct., Río Guamól, 2 (MSB); 6 mi. S Matias Romero, Río Grande, 4 (USNM); 9.5 mi. S Matias Romero, 2 (TTU); Pochutla, Puerto Angel, 100-200 ft., 1 (USNM); Potrero de Villalobos, 1 (AMNH); 4-7 mi. S Putla, 2500-2700 ft., 4 (MSU); 4 mi. E Tapanatepec, ca. 800 ft., 1 (TCWC); 10 mi. S Tapanatepec, 3 (AMNH); 4 mi. WNW Tapanatepec, 7 (AMNH); 20 mi. W Tapanatepec, Hwy. 190, 3 (UA); 1 mi. N Tequistitlán, ca. 800 ft., 1 (TCWC); Unión Hidalgo, 2 (AMNH); 9.5 mi. W Zanatepec at km. post 889, El Guamól, 1 (USNM); Zanatepec, 14 (AMNH). *Tlaxcala*: 13 km. NE Tlaxcala, 7800 ft., 2 (TCWC). *Veracruz*: Achotal, 1 (LACM). NICARAGUA. *Boaco*: San Francisco, km. 92 on Rama Rd., 400 ft., 1 (TCWC); 4 km. W Teustepe, 140 m., 2 (KU). *Chontales*: Haio Grande, 13 km. S, 8

km. W Juigalpa, 60 m., 2 (KU); *Granada*: Granada, 1 (FMNH). *Isla de Ometepe*: 6 km. E Moyogalpa, 400 m., 1 (KU). *Madriz*: 7 km. N, 14 km. E Condega, 1325 m., 2 (KU). *Managua*: 3 mi. SW Managua, 6 (KU); 1 km. N Sabana Grande, 40 m., 1 (KU). *Matagalpa*: 2 mi. SE Dario, 1500 ft., 2 (TCWC); 3 mi. W Matagalpa, 2300 ft., 2 (TCWC). *Rivas*: 15 mi. NE San Juan del Sur, 50 m., 2 (KU).

Additional records.—MEXICO. *Morelos*: Tlayacapan, 1950 m. (Eguiarte *et al.*, 1987).

Marginal records.—MEXICO. *Colima*: Comala. *Jalisco*: 10 mi. NNE Pihuamo, 3500 ft. *Tlaxcala*: 13 km. NE Tlaxcala, 7800 ft. *Veracruz*: Achotal. *Chiapas*: 5 km. ESE Pichucalco, 200 ft. GUATAMALA. *El Progreso*: El Progreso. HONDURAS. *Ocotepeque*: 4 km. N Nueva Ocotepeque, 480 m. *El Paraíso*: Chichicaste, 480 m. NICARAGUA. *Chontales*: Hato Grande, 13 km. S, 8 km. W Juigalpa, 60 m. COSTA RICA. *Cartago*: Tres Rios, 400 ft.

Glossophaga longirostris

Miller's Long-tongued Bat

The geographic distribution of *G. longirostris* includes northern South America (Colombia eastward to Guyana) and several of the Caribbean islands immediately adjacent to the mainland, including the Netherlands Antilles (Aruba, Curaçao, and Bonaire), the continental islands of Margarita, Trinidad, and Tobago, and the southern Lesser Antilles from Grenada northward to St. Vincent (except Barbados). Hummelinck (1940) reported *G. soricina* from the Testugos and several of the islands mentioned above. Some or all of these bats may represent *G. longirostris* (see Koopman, 1958), although Webster and Handley (1986) reported *G. soricina* from Isla Margarita, Grenada, and Bequia.

Diagnosis

Largest member of the genus in most external and cranial measurements; upper incisors noticeably and equally procumbent, I2 equal to I1 in bulk (occlusal view); P4 with reduced lingual cingular shelf; M1 narrow; parastyle of M1 usually absent or, if present, minute and directed posterolabially from paracone; mesostyle of M1 reduced, continuous with labial outline of tooth; fourth commissure of M1 long, well developed, and always longer than third; M2 similar to M1 except parastyle better developed, directed labially; lower incisors large and usually in contact, subtriangular in occlusal view, equal in bulk; p4 narrow, similar to p2 and p3 in bulk; premaxillae elongate anteriorly; pterygoid alae absent; presphenoid ridge usually high and complete throughout; mandibular symphyseal ridge absent, chin of mandible receding at a 45° angle; pelage bicolored, the tips of the individual hairs darker than the paler bases, Wood Brown to Fuscous dorsally, Avellaneous to Clove Brown ventrally; weight averaging 13.3 (10.3-16) grams in males, 12.8 (9.8-14.3) grams in nonparous females from throughout the range of the species.

Comparisons

Characters that separate *Glossophaga longirostris* from *G. commissarisi* and *G. leachii* are in those respective accounts. Specimens of *G. longirostris* can be distinguished from those of *G. morenoi* by their larger size, both externally and cranially; the presphenoid ridge is high and complete throughout in *G. longirostris*, but flattened subterminally in *G. morenoi*; the mandibular symphyseal ridge is absent in *G. longirostris*, but pronounced in *G. morenoi*; the canines and upper incisors are larger in *G. longirostris* than those of *G. morenoi*; the lower incisors are large, in contact, and equal in bulk (occlusal view) in *G. longirostris*, but reduced in size, evenly spaced between the canines, the outer pair the larger in *G. morenoi*. In addition, in *G. longirostris* the mesostyle of M2 is greatly reduced, causing the labial outline of the tooth to be gently bowed outward at the parastyle and metastyle. The mesostyle of M2 in *G. morenoi* is well developed and the labial outline of the tooth is W-shaped.

Glossophaga longirostris can be distinguished from *G. soricina* by its larger size in most external and cranial measurements, particularly in northern South America where the two species are sympatric. The pterygoid alae and mandibular symphyseal ridge are absent in *G. longirostris* (well developed in *G. soricina*); the upper incisors are similar in bulk in *G. longirostris* (I2 smaller than I1 in *G. soricina*); the lingual cingular shelf of P4 is reduced in *G. longirostris* (prominent in *G. soricina*); the parastyle of M1 is absent in *G. longirostris* (well developed and directed anterolabially in *G. soricina*); the mesostyles of M1 and M2 are poorly developed in *G. longirostris* (well developed in *G. soricina*); and p4 is narrow and similar to p2 and p3 in bulk in *G. longirostris* (p4 wider than p2 and p3 in *G. soricina*). Tamsitt and Valdivieso (1963) reported the noseleaf of *G. longirostris* to be smaller than that of sympatric *G. soricina* in central Colombia, but specimens of both species from the savannas of the Rupununi in Guyana and the llanos of Venezuela showed the opposite relationship (specimens from each locality were collected on the same day and preserved in fluid in identical manner): the noseleaf of *G. longirostris* averaged 6.1 (5.7-6.4), whereas that of *G. soricina* averaged 5.3 (4.6-5.7) (Webster and Handley, 1986).

Ecology and Reproduction

Glossophaga longirostris is found in various tropical and subtropical habitats in northern South America including arid thorn forests, deciduous and evergreen forests, and savannas. In Venezuela (Handley, 1976), individuals were collected most frequently in dry areas (65 percent) or near streams and other moist areas (35 percent); in thorn forest (49 percent) or savannas and other open areas (43 percent); in tropical dry forest (43 percent), tropical thorn forest (35 percent), or tropical very dry forest (17 percent). Daytime roosts include caves, tunnels, culverts, crevices in rocks, hollow trees, and houses and other buildings. Specimens have been captured

from sea level to approximately 650 meters in elevation, but most records are from less than 500 meters. Ecological observations can be found in G. M. Allen (1902, 1911), J. A. Allen (1900, 1911), Genoways and Williams (1979a), Goodwin and Greenhall (1961), Handley (1976), Husson (1954), Jones (1951), Miller (1898, 1900a, 1900b, 1913a), Pirlot (1963, 1964), Pirlot and León (1965), Robinson and Lyon (1901), Smith and Genoways (1974), Tamsitt and Valdivieso (1963), Valdivieso (1964), and Webster and Handley (1986).

Other bats known to share daytime roosts with *G. longirostris* include *Peropteryx macrotis*, *Micronycteris megalotis*, *Phyllostomus hastatus*, *Glossophaga soricina*, and *Carollia perspicillata*. These species, *P. discolor*, and *Artibeus lituratus* have been collected in the same mist nets in Colombia.

One-hundred and forty-seven *G. longirostris* from Colombia were rabies negative (Morales-Alarcón *et al.*, 1968). Labidocarpid (*Alabidocarpus furmani*, *Parakosa maxima*, and *P. tadarida*), spinturnicid (*Pergilischurs caligus*), and trombiculid (*Eutrombicula goeldi* and *Loomisia desmodus*) mites are known to parasitize *Glossophaga longirostris*, as do argasid (*Ornithodoros azteci*, *O. hasei*, and *O. rossi*) and ixodid (*Amblyomma* sp.) ticks (Webb and Loomis, 1977).

The reproductive strategy of *Glossophaga longirostris* appears to be that of monotocous polyestry with a bimodal cycle (Webster and Handley, 1986). Peak periods of pregnancy extend from December to April and from June to October; lactating females have been collected in every month except February (Fig. 13).

Geographic Variation

Univariate Analyses

Adult specimens from throughout the geographic range of *G. longirostris* were grouped into 13 samples (see Fig. 14) as follows: *sample 1*—ARUBA (males only); *sample 2*—CURAÇAO; *sample 3*—BONAIRE; *sample 4*—TRINIDAD; *sample 5*—TOBAGO; *sample 6*—GRENADA; *sample 7*—ST. VINCENT; *sample 8*—COLOMBIA (upper Magdalena River Valley); *sample 9*—COLOMBIA (Bolívar, Magdalena, and Sucre) and VENEZUELA (Falcón); *sample 10*—VENEZUELA (Nueva Esparta); *sample 11*—VENEZUELA (Falcón, Guárico, Miranda, and Sucre); *sample 12*—VENEZUELA (T. F. Amazonas, Apure, and Bolívar); *sample 13*—GUYANA. Standard statistics for all geographic samples are given in Table 12, and the results of four (length of forearm, condylobasal length, zygomatic breadth, and depth of brain-case) SS-STP tests are given in Table 13.

External measurements.—Specimens from the upper Magdalena Valley (*sample 8*) average much larger than those of other populations in measurements of the wing. Bats from Trinidad (*sample 4*), particularly the females, northern Colombia and northwestern Venezuela (*9*), and the males from Aruba (*1*) and Bonaire (*3*) are moderately large, whereas those from Tobago (*5*), Grenada (*6*), northern Venezuela (*11*), Margarita Island (*10*), and Guyana (*13*) have wing measurements that average

in the middle of the range for the species. Specimens from Curaçao (2), St. Vincent (7), central Venezuela (12), and the one female from Bonaire (3) average smaller than those from other populations in measurements of the wing.

Cranial measurements.—Specimens from the Netherlands Antilles (1-3), Magdalena Valley of Colombia (8), and northern Colombia and northwestern Venezuela (9) average larger than bats in all other samples in greatest length of skull, condylobasal length, length of rostrum, length of maxillary and mandibular toothrows, and mandibular length. Specimens from central Venezuela (12) are much smaller than average for the species, whereas those from Trinidad (4), Tobago (5), Grenada (6), St. Vincent (7), Margarita Island (10), northern Venezuela (11) and Guyana (13) average in the middle of the range in measurements that reflect cranial length.

Specimens from Colombia and northwestern Venezuela (8-9) and Trinidad (4) average larger than those in other samples in zygomatic breadth, mastoid breadth, and breadth of braincase. Specimens from samples 1-3 (Netherlands Antilles) and 12 (central Venezuela) are much smaller than average, and bats from samples 5-7 (Tobago, Grenada, and St. Vincent), 10 (Margarita Island), 11 (northern Venezuela), and 13 (Guyana) average in the middle of the range for the species in zygomatic breadth, mastoid breadth, and breadth of braincase.

Patterns of geographic variation in interorbital breadth are similar to those described in the preceding paragraph except that specimens from Trinidad (4) average in the middle of the range for the species, those from Grenada (6) and St. Vincent (7) are smaller than average, and those from Tobago (5) are larger than average.

Specimens from samples 4 (Trinidad), 8-9 (Colombia and northwestern Venezuela), and 13 (Guyana) average larger than those of all other samples in depth of braincase, and specimens from the Netherlands Antilles (1-3) have means that are smaller than average. Bats from Tobago (5), Grenada (6), St. Vincent (7), Margarita Island (10), and northern and central Venezuela (11-12) average in the middle of the range for the species.

The pattern of geographic variation in width across molars appears unique in *G. longirostris*. Specimens from Colombia and northwestern Venezuela (8-9) and the males from Aruba (1) and Bonaire (3) are much broader than average for the species in this measurement, whereas those from Trinidad (4), Tobago (5), Grenada (6), St. Vincent (7), and central Venezuela (12) are narrower than average. Bats from Curaçao (2), Margarita Island (10), northern Venezuela (11), Guyana (13), and the female from Bonaire (3) are in the middle of the range for the species.

Pelage coloration.—Specimens from Trinidad (4), Tobago (5), and St. Vincent (7) are darker than those from Colombia and northwestern Venezuela (8-9), but paler in color than individuals from Curaçao (2), Margarita Island (10), Grenada (6), northern and central Venezuela (11-12), and Guyana (13). Color was not deter-

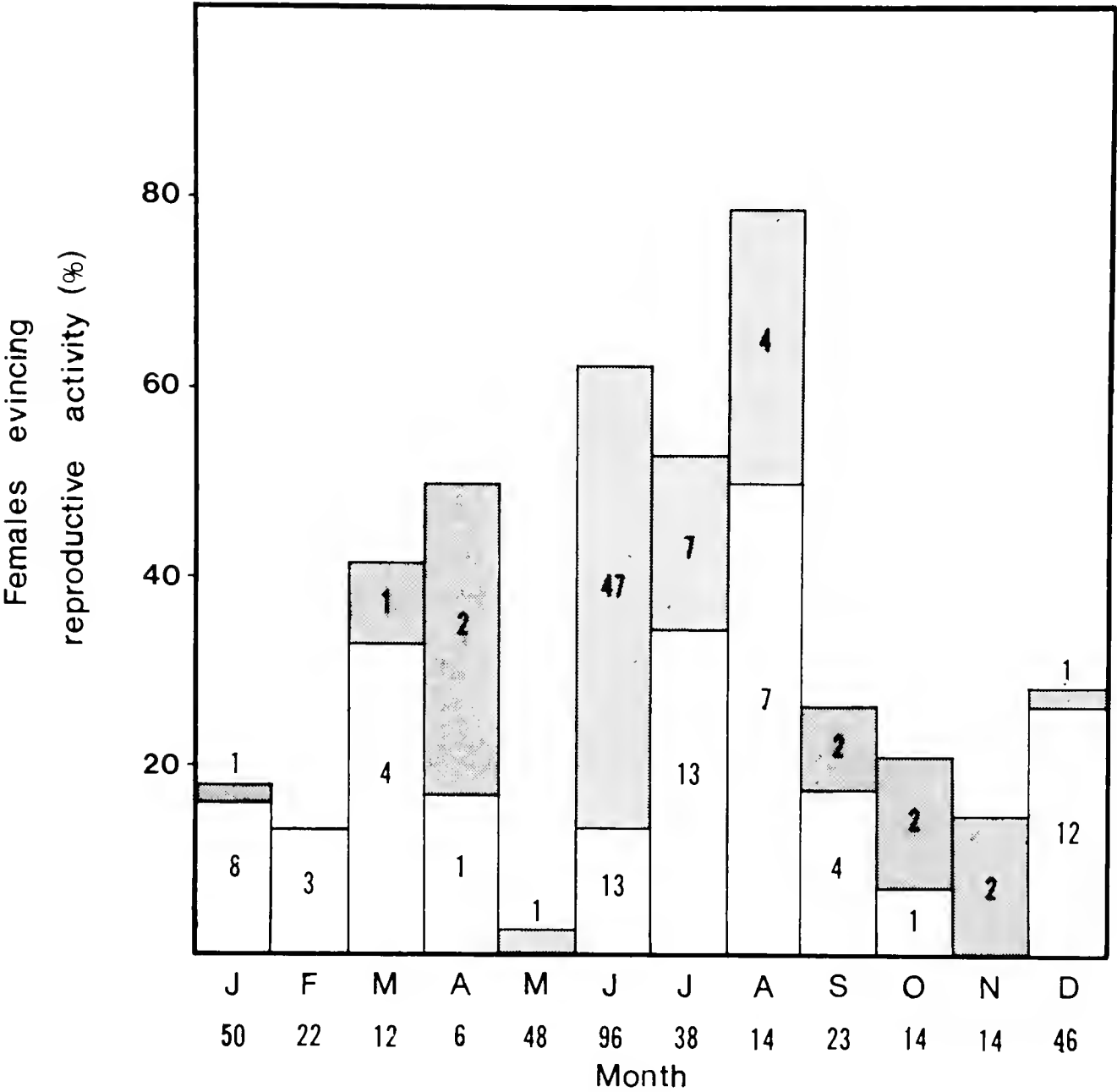


FIG. 13.—Reproductive activity in *Glossophaga longirostris*. The histogram represents the percent of 231 females evincing pregnancy (open) or lactation (stipple) each month; the number of pregnant and lactating females are in the histogram, and the total number of females examined are shown below each month.

mined for specimens from Aruba (1) and Bonaire (3) because the skins examined were preserved in fluid.

Qualitative cranial characters (Table 5).—Pterygoid alae were absent in 86.6 percent of the specimens of *Glossophaga longirostris* examined by me, being modestly developed in 13 (6.4 percent) and well developed in 14 (6.9 percent) of 202 individuals examined. Specimens from Trinidad (4) and the Magdalena Valley (8) most often have moderately-developed pterygoid alae; those from Bonaire (3) and central Venezuela (12) have the highest incidence of well-developed alae. No individuals examined from Curaçao (2), Grenada (6), St. Vincent (7), Margarita Island (10), or Guyana (13) possessed pterygoid alae.

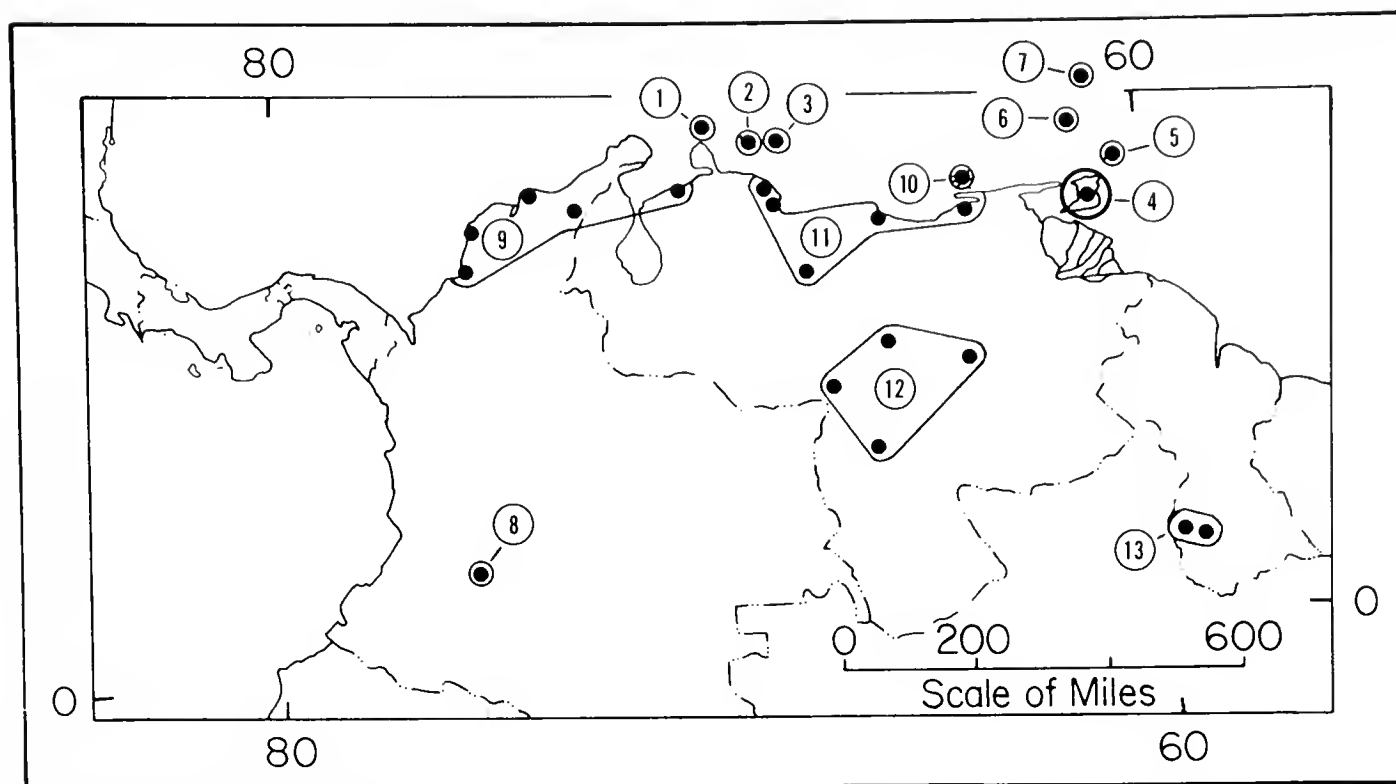


FIG. 14.—Approximate geographic areas included in the 13 samples of *Glossophaga longirostris* analyzed. See text for localities in each sample.

The presphenoid ridge was high and complete throughout in 72.4 percent of 203 *G. longirostris* examined, particularly in specimens from St. Vincent (7), where all bats exhibited a continuous ridge. The ridge was moderately developed in 22.2 percent of the specimens examined; most individuals from samples 2 (Curaçao), 5 (Tobago), 6 (Grenada), 9 (northern Colombia and northwestern Venezuela), 10 (Margarita Island), and 13 (Guyana) possessed a moderately-developed ridge. Specimens from central Venezuela (12) and the male from Bonaire (3) have presphenoid ridges that are flattened subterminally relative to those in other samples.

The upper incisors were noticeably procumbent in 181 of 194 (93.3 percent) *G. longirostris* examined, particularly in individuals from Trinidad (4), Colombia and northwestern Venezuela (8-9), Margarita Island (10), and Guyana (13), in which all specimens exhibited this character. Upper incisors are moderately procumbent in 13 (6.7 percent) of the specimens examined, seven of which were from Grenada (6) and St. Vincent (7).

The upper incisors are equal (55.7 percent) or subequal (20.1 percent) in bulk in *G. longirostris*, except in specimens from Trinidad (4), Tobago (5), Grenada (6), and St. Vincent (7), in which the upper incisors tend to be unequal, the inner pair the larger. The latter samples constituted 45 of the 47 individuals of *G. longirostris* that have unequal upper incisors.

Basisphenoid pits are deep (47.0 percent) or moderately deep (43.0 percent) in *G. longirostris*. Shallow pits are most common in specimens examined from Curaçao (2) and Margarita Island (10), particularly the females. Individuals from Trinidad

TABLE 12.—*Geographic variation in external and cranial measurements among 13 samples of Glossophaga longirostris. See text and Figure 14 for key to sample numbers.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of forearm</i>								
1	1	39.00						
2	13	36.65	35.3–38.1	1.73	14	37.41	36.4–38.8	1.54
3	1	38.10			1	37.00		
4	2	38.65	37.5–39.8	3.25	12	39.45	38.0–41.9	2.08
5	3	38.37	38.0–38.6	0.64	7	38.69	37.6–39.6	1.52
6	10	37.50	35.4–39.8	2.41	9	38.30	37.1–39.5	1.54
7	10	37.62	36.1–39.9	2.35	10	37.24	36.1–38.6	1.34
8	9	39.73	38.6–41.3	1.84	12	40.13	38.7–41.6	1.84
9	10	38.22	37.3–39.8	1.47	5	38.90	37.7–39.8	1.81
10	5	37.30	35.9–38.5	2.21	7	38.13	36.4–39.5	2.42
11	17	37.66	35.7–39.2	1.82	14	38.14	37.2–39.3	1.23
12	7	37.07	36.6–37.8	0.73	7	37.27	36.3–38.0	1.40
13	2	37.95	37.5–38.4	1.27	9	38.40	37.1–40.1	2.00
<i>Length of third metacarpal</i>								
1	1	39.10						
2	13	37.72	36.3–39.3	1.84	14	37.99	36.8–39.7	1.84
3	1	39.40			1	38.30		
4	2	38.05	37.6–38.5	1.27	12	39.31	38.0–40.3	1.31
5	3	38.13	37.2–38.8	1.67	7	38.29	37.5–38.8	0.96
6	10	37.29	36.0–38.7	1.62	9	38.26	37.4–39.2	1.33
7	10	37.48	36.6–39.4	1.68	10	37.94	36.6–39.0	1.38
8	9	40.21	38.8–41.2	1.57	13	40.17	38.3–41.8	2.16
9	10	38.04	36.9–39.7	1.68	5	39.02	37.7–39.8	1.99
10	5	37.60	36.0–39.5	2.98	7	38.00	36.7–39.1	1.84
11	17	37.83	36.4–40.0	1.85	14	37.87	36.4–39.1	1.79
12	7	36.89	36.0–37.6	1.33	7	37.33	36.2–38.4	1.45
13	2	37.95	37.6–38.3	0.99	9	38.10	37.2–39.0	1.25
<i>Length of fourth metacarpal</i>								
1	1	35.10						
2	13	34.31	33.2–35.7	1.42	14	34.61	33.2–36.1	1.84
3	1	35.90			1	34.30		
4	2	35.50	35.3–35.7	0.57	12	36.15	34.7–37.1	1.32
5	3	34.80	33.6–35.9	2.31	7	35.06	33.8–36.1	1.64
6	10	34.46	33.3–35.8	1.53	9	35.62	34.4–39.5	3.09
7	10	34.66	33.5–36.3	2.00	10	34.61	33.4–35.7	1.38
8	9	37.44	36.1–39.1	1.97	12	36.93	35.7–38.4	1.82
9	10	35.12	33.9–36.6	1.44	5	36.00	34.9–36.7	1.34
10	5	34.46	33.1–35.7	2.29	7	35.06	34.0–36.7	2.21
11	17	34.92	33.9–36.6	1.66	14	34.72	33.9–35.6	1.25
12	7	34.06	33.3–35.2	1.43	7	33.99	32.5–35.8	2.38
13	2	34.75	34.2–35.3	1.56	9	35.47	34.5–37.2	1.84

TABLE 12.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of fifth metacarpal</i>								
1	1	34.80						
2	13	33.75	32.0–35.1	1.83	14	34.15	33.0–35.8	1.54
3	1	34.60			1	34.20		
4	2	35.25	35.0–35.5	0.71	12	35.71	34.2–36.5	1.28
5	3	34.50	34.2–34.8	0.60	7	34.50	33.5–35.3	1.33
6	10	33.73	32.5–34.4	1.16	9	35.00	33.6–39.5	3.52
7	10	33.58	32.2–35.6	1.88	10	34.03	33.2–35.0	1.17
8	9	36.80	35.9–38.1	1.30	13	36.77	35.4–38.3	1.80
9	10	34.58	32.9–34.6	1.76	5	35.72	34.4–36.8	1.93
10	5	33.94	32.9–34.6	1.47	7	34.60	33.1–36.7	2.80
11	17	34.21	32.6–36.2	1.76	14	34.32	33.0–35.6	1.51
12	7	33.19	32.3–34.5	1.41	7	33.74	32.5–34.8	1.49
13	2	33.55	33.2–33.9	0.99	9	34.69	33.4–36.3	1.76
<i>Greatest length of skull</i>								
1	1	24.40						
2	14	23.38	22.5–23.9	0.72	14	23.82	23.3–24.6	0.70
3	1	24.50			1	24.00		
4	4	22.85	22.4–23.5	1.04	8	23.18	22.6–24.0	0.85
5	3	23.00	22.8–23.4	0.69	5	22.78	22.6–23.0	0.36
6	7	22.79	22.6–22.9	0.24	9	23.14	22.8–23.4	0.43
7	8	22.85	22.6–23.7	0.72	10	22.79	22.4–23.2	0.51
8	9	24.01	23.6–24.6	0.69	13	24.18	23.5–24.8	0.91
9	11	23.45	23.0–24.0	0.71	6	23.67	23.2–24.4	1.07
10	5	22.98	22.6–23.7	0.89	7	23.03	22.5–23.6	0.90
11	17	22.96	22.5–23.8	0.67	14	23.06	22.4–23.7	0.81
12	9	22.18	21.6–22.6	0.62	7	22.39	22.1–22.7	0.47
13	2	22.50	22.2–22.8	0.85	9	23.06	22.6–23.6	0.69
<i>Condylobasal length</i>								
1	1	23.00						
2	14	21.72	20.9–22.2	0.76	14	22.14	21.7–22.6	0.69
3	1	23.10			1	22.60		
4	4	21.10	20.6–21.6	0.88	8	21.50	21.0–22.2	0.77
5	3	21.60	21.3–22.0	0.72	5	21.52	21.1–22.1	0.75
6	7	21.24	20.9–21.8	0.69	9	21.54	21.3–21.7	0.32
7	8	21.15	20.8–22.2	0.93	10	21.19	20.9–21.9	0.57
8	9	22.47	22.1–22.9	0.50	12	22.65	22.0–23.0	0.58
9	11	21.92	21.4–22.4	0.70	6	22.18	21.7–22.9	1.13
10	5	21.24	20.4–21.9	1.11	7	21.51	21.0–22.0	0.73
11	17	21.18	20.4–22.2	0.91	14	21.49	20.8–22.2	0.82
12	9	20.40	19.9–20.9	0.58	7	20.73	20.2–21.2	0.61
13	2	20.85	20.7–21.0	0.42	9	21.31	20.8–22.3	0.94

TABLE 12.—*Continued.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Zygomatic breadth</i>								
1	1	9.90						
2	12	9.41	9.2–9.7	0.31	14	9.44	9.2–9.8	0.34
3	1	9.50			1	9.70		
4	3	10.00	9.8–10.2	0.40	9	10.06	9.8–10.4	0.38
5	3	9.33	9.8–10.0	0.23	4	9.78	9.6–10.0	0.41
6	9	9.87	9.5–10.1	0.37	7	9.71	9.4–10.2	0.58
7	10	9.83	9.5–10.3	0.55	10	9.64	9.5–9.9	0.32
8	9	10.40	10.1–10.6	0.36	13	10.28	9.6–10.6	0.60
9	10	9.99	9.5–10.4	0.62	5	10.22	9.9–10.5	0.43
10	5	9.92	9.6–10.3	0.52	7	9.84	9.5–10.1	0.40
11	17	9.93	9.4–10.6	0.67	14	9.80	9.5–10.2	0.40
12	9	9.51	9.2–10.1	0.61	7	9.69	9.4–10.0	0.37
13	2	9.70	9.7	0.00	9	10.00	9.6–10.4	0.52
<i>Length of rostrum</i>								
1	1	10.00						
2	14	9.41	9.2–9.7	0.31	14	9.51	9.2–9.7	0.35
3	1	10.00			1	9.10		
4	4	9.33	9.1–9.5	0.41	12	9.33	9.2–9.7	0.30
5	3	9.30	9.2–9.5	0.23	7	9.36	9.1–9.6	0.32
6	8	9.16	9.0–9.3	0.24	10	9.30	9.1–9.7	0.34
7	9	8.99	8.8–9.3	0.55	10	8.98	8.8–9.3	0.32
8	9	9.78	9.5–10.1	0.36	13	9.82	9.5–10.1	0.40
9	11	9.42	9.1–9.8	0.53	6	9.58	9.3–10.0	0.58
10	5	9.10	8.7–9.7	0.76	7	9.33	9.1–9.6	0.36
11	17	9.06	8.7–9.5	0.41	14	9.26	8.9–9.8	0.51
12	9	8.70	8.3–9.0	0.42	7	8.87	8.6–9.1	0.34
13	2	9.00	8.8–9.2	0.57	9	9.17	8.9–9.6	0.45
<i>Mastoid breadth</i>								
1	1	9.10						
2	14	8.84	8.5–9.2	0.36	14	9.05	8.9–9.2	0.23
3	1	9.10			1	9.10		
4	4	9.38	9.1–9.6	0.53	7	9.47	9.3–9.6	0.22
5	3	9.47	9.4–9.5	0.12	4	9.43	9.3–9.5	0.19
6	8	9.44	9.3–9.7	0.26	7	9.43	9.0–9.6	0.43
7	9	9.48	9.2–9.9	0.42	10	9.28	9.1–9.4	0.18
8	9	9.67	9.4–9.9	0.32	12	9.68	9.4–10.0	0.39
9	12	9.42	9.1–9.7	0.42	6	9.52	9.2–9.8	0.41
10	5	9.34	8.9–9.6	0.58	7	9.30	9.0–9.5	0.37
11	17	9.38	9.0–9.9	0.49	14	9.33	8.9–9.8	0.46
12	9	9.02	8.8–9.4	0.41	7	9.23	9.1–9.4	0.19
13	2	9.40	9.3–9.5	0.28	9	9.47	9.2–9.8	0.41

TABLE 12.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Interorbital breadth</i>								
1	1	4.20						
2	14	4.23	4.0–4.6	0.31	14	4.23	4.1–4.4	0.20
3	1	4.40			1	4.20		
4	4	4.35	4.2–4.5	0.26	11	4.33	4.1–4.6	0.27
5	3	4.50	4.3–4.7	0.40	7	4.34	4.2–4.5	0.20
6	9	4.27	4.1–4.4	0.20	10	4.24	3.9–4.4	0.29
7	10	4.22	4.1–4.3	0.16	10	4.28	4.1–4.5	0.23
8	9	4.52	4.4–4.7	0.16	13	4.43	4.2–4.8	0.33
9	12	4.33	4.0–4.5	0.27	6	4.40	4.3–4.5	0.18
10	5	4.40	4.1–4.6	0.37	7	4.39	4.2–4.6	0.27
11	17	4.40	4.2–4.7	0.34	14	4.29	4.1–4.5	0.21
12	9	4.28	4.0–4.6	0.33	7	4.26	4.1–4.4	0.23
13	2	4.35	4.2–4.5	0.42	9	4.36	4.0–4.6	0.35
<i>Breadth of braincase</i>								
1	1	8.60						
2	14	8.54	8.3–8.8	0.38	14	8.57	8.3–8.8	0.34
3	1	8.20			1	8.40		
4	4	9.08	9.0–9.1	0.10	6	9.00	8.8–9.2	0.25
5	3	8.73	8.6–8.8	0.23	4	8.70	8.6–8.8	0.23
6	10	8.78	8.5–8.9	0.26	7	8.97	8.7–9.4	0.44
7	10	8.77	8.6–9.0	0.33	10	8.66	8.4–8.9	0.29
8	9	9.01	8.9–9.3	0.29	11	8.99	8.6–9.4	0.42
9	12	8.96	8.6–9.3	0.44	6	9.08	8.7–9.3	0.54
10	5	8.88	8.4–9.2	0.59	7	8.90	8.6–9.3	0.48
11	17	8.99	8.6–9.6	0.52	14	8.87	8.7–9.2	0.31
12	9	8.72	8.4–9.1	0.47	7	8.74	8.4–8.9	0.38
13	2	9.00	8.9–9.1	0.28	9	8.93	8.8–9.1	0.26
<i>Depth of braincase</i>								
1	1	6.80						
2	14	6.65	6.3–7.0	0.36	14	6.66	6.4–6.9	0.29
3	1	6.60			1	6.60		
4	4	7.28	7.1–7.4	0.25	6	7.38	7.2–7.5	0.23
5	3	7.07	7.0–7.1	0.12	4	7.03	6.9–7.2	0.25
6	9	7.08	6.8–7.3	0.28	9	7.20	6.9–7.4	0.33
7	8	7.18	7.1–7.3	0.14	10	7.15	7.0–7.3	0.22
8	9	7.38	7.1–7.7	0.38	10	7.32	6.8–7.7	0.49
9	12	7.23	7.0–7.6	0.43	6	7.37	7.0–7.6	0.43
10	5	7.36	6.9–8.2	1.00	7	7.19	7.0–7.3	0.27
11	17	7.30	7.0–7.8	0.44	14	7.17	6.9–7.5	0.31
12	9	7.21	7.0–7.6	0.34	7	7.19	7.0–7.4	0.31
13	2	7.35	7.3–7.4	0.14	9	7.31	7.1–7.5	0.25

TABLE 12.—*Continued.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of maxillary toothrow</i>								
1	1	8.40						
2	14	7.92	7.5–8.1	0.39	14	8.06	7.8–8.4	0.33
3	1	8.50			1	8.40		
4	4	8.00	7.9–8.1	0.16	12	7.98	7.6–8.4	0.46
5	3	7.73	7.6–7.9	0.31	7	7.74	7.6–7.9	0.20
6	10	7.85	7.7–8.0	0.22	10	7.98	7.8–8.2	0.26
7	10	7.68	7.5–8.0	0.34	10	7.81	7.6–8.1	0.33
8	9	8.37	8.0–8.7	0.42	13	8.45	8.2–8.7	0.34
9	10	7.96	7.6–8.2	0.33	6	8.20	7.9–8.7	0.59
10	5	7.90	7.5–8.4	0.65	7	8.04	7.8–8.3	0.34
11	17	7.85	7.5–8.3	0.41	14	7.99	7.6–8.5	0.57
12	9	7.51	7.3–7.7	0.27	7	7.69	7.5–7.9	0.27
13	2	7.90	7.7–8.1	0.57	9	8.02	7.7–8.2	0.37
<i>Length of mandibular toothrow</i>								
1	1	8.80						
2	14	8.41	7.9–8.7	0.46	14	8.44	8.1–8.8	0.34
3	1	8.80			1	8.70		
4	4	8.50	8.3–8.6	0.28	12	8.38	8.1–8.7	0.17
5	3	8.17	8.0–8.3	0.31	7	8.07	8.0–8.2	0.19
6	10	8.30	8.0–8.5	0.22	10	8.35	8.2–8.5	0.24
7	10	8.11	7.9–8.5	0.43	10	8.18	8.0–8.4	0.30
8	9	8.88	8.5–9.1	0.36	13	8.91	8.5–9.2	0.41
9	10	8.50	8.0–8.7	0.46	6	8.60	8.4–8.9	0.46
10	5	8.42	8.2–8.8	0.46	7	8.44	8.1–8.7	0.43
11	17	8.35	8.0–8.9	0.45	14	8.44	8.1–9.0	0.57
12	9	7.93	7.7–8.2	0.35	7	8.09	7.7–8.4	0.42
13	2	8.35	8.1–8.6	0.71	9	8.02	8.0–8.7	0.46
<i>Width across molars</i>								
1	1	6.30						
2	14	5.90	5.4–6.1	0.67	14	5.89	5.7–6.1	0.25
3	1	6.20			1	6.00		
4	4	5.83	5.7–5.9	0.19	11	5.83	5.5–6.1	0.37
5	3	5.77	5.6–5.9	0.31	7	5.67	5.6–5.9	0.22
6	10	5.86	5.6–6.1	0.30	10	5.78	5.5–6.1	0.41
7	10	5.81	5.6–6.0	0.29	10	5.82	5.6–6.0	0.25
8	9	6.30	6.1–6.6	0.30	13	6.35	6.0–6.6	0.34
9	9	6.03	5.8–6.4	0.37	5	6.26	6.1–6.4	0.23
10	5	5.80	5.7–6.0	0.25	7	5.93	5.8–6.1	0.22
11	17	5.99	5.5–6.5	0.42	14	5.86	5.4–6.2	0.40
12	9	5.70	5.4–6.0	0.34	7	5.80	5.5–6.0	0.38
13	2	5.95	5.8–6.1	0.42	9	5.96	5.8–6.2	0.27

TABLE 12.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
Mandibular length								
1	1	15.90						
2	14	15.06	14.5–15.5	0.67	14	15.26	14.9–15.7	0.46
3	1	16.20			1	16.00		
4	4	14.80	14.5–15.1	0.59	9	15.02	14.7–15.4	0.61
5	3	14.93	14.6–15.2	0.61	7	14.84	14.5–15.1	0.49
6	9	14.71	14.3–15.0	0.44	9	15.02	14.7–15.4	0.44
7	9	14.62	14.3–15.6	0.85	10	14.57	14.3–15.0	0.40
8	9	15.81	15.4–16.4	0.66	13	15.93	15.0–16.3	0.75
9	10	15.40	14.9–15.9	0.60	6	15.55	15.2–16.0	0.71
10	5	15.02	14.6–15.6	0.79	7	15.16	14.8–15.5	0.50
11	17	14.90	14.6–15.6	0.62	14	15.08	14.5–15.7	0.65
12	9	14.27	13.9–14.6	0.40	7	14.59	14.2–14.9	0.51
13	1	14.70			9	14.89	14.4–15.4	0.75

(4), Tobago (5), and the Magdalena Valley of Colombia (8) tend to have basi-sphenoid pits that are moderately deep relative to bats in other samples.

The upper premolars are unequal (45.4 percent) or subequal (41.5 percent) in bulk, the second being larger than the first. Specimens from Guyana (13), the male from Aruba (1), and the female from Bonaire (3) have upper premolars that are equal in bulk relative to those from other samples. I found tremendous variation in this character, however. Miller (1913*b*) used the shape of the upper premolars to distinguish between *G. longirostris* and *G. soricina*, but he noted that some specimens referable to both species were indistinguishable on the basis of the upper premolars.

The lower incisors in *G. longirostris* are large and in contact (88.8 percent), or medium-sized and evenly spaced between the canines (11.2 percent). All specimens from Bonaire (3), Margarita Island (10), and Guyana (13) have lower incisors that are large and in contact. Lower incisors average medium in size in specimens from Tobago (5) and the male from Aruba (1).

The slope of the forehead is continuous (41.4 percent) or gradual (58.6 percent) in *G. longirostris*, being continuous most frequently in specimens from the Netherlands Antilles (1-3) and Margarita Island (10). The slope from the rostrum to brain-case is most pronounced in specimens from Trinidad (4), Grenada (6), Colombia and northwestern Venezuela (8-9).

Posterior palatine processes are poorly developed (53.4 percent), moderately developed (14.7 percent), or greatly developed (21.1 percent) in *G. longirostris*. Specimens from the Magdalena Valley (8) and the female from Bonaire (3) most

TABLE 13.—Results of four SS–STP tests of geographic variation in *Glossophaga longirostris*. Vertical lines to the right of sample means connect maximally nonsignificant subsets at the 0.05 probability level for length of forearm, condylobasal length, zygomatic breadth, and depth of braincase. See text and Figure 14 for key to sample numbers.

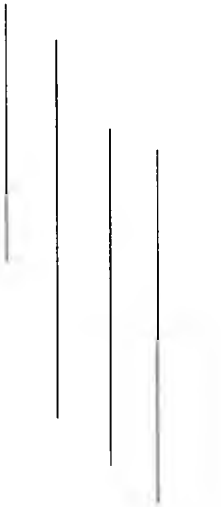
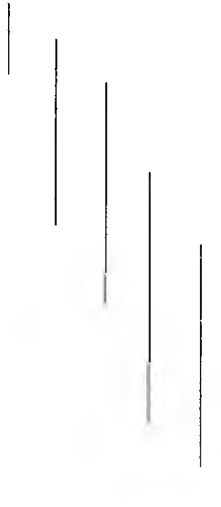




Sample number	Males		Sample number	Females	
	Mean	Results SS-STP		Mean	Results SS-STP
Length of forearm					
8	39.73		8	40.13	
1	39.00		4	39.45	
4	38.65		9	38.90	
5	38.37		5	38.69	
9	38.22		13	38.40	
3	38.10		6	38.30	
13	37.95		11	38.14	
11	37.66		10	38.13	
7	37.62		2	37.41	
6	37.50		12	37.27	
10	37.30		7	37.24	
12	37.07		3	37.00	
2	36.65				
Condylobasal length					
3	23.10		8	22.65	
1	23.00		3	22.60	
8	22.47		9	22.18	
9	21.92		2	22.14	
2	21.72		6	21.54	
5	21.60		5	21.52	
6	21.24		10	21.51	
10	21.24		4	21.50	
11	21.18		11	21.49	
7	21.15		13	21.31	
4	21.10		7	21.19	
13	20.85		12	20.73	
12	20.40				
Zygomatic breadth					
8	10.40		8	10.28	
4	10.00		9	10.22	
9	9.99		4	10.06	
5	9.93		13	10.00	
11	9.93		10	9.84	
10	9.92		11	9.80	
1	9.90		5	9.78	
6	9.87		6	9.71	
7	9.83		3	9.70	
13	9.70		12	9.69	
12	9.51		7	9.64	
3	9.50		2	9.44	
2	9.41				

TABLE 13.—Continued.

Sample number	Males		Sample number	Females	
	Mean	Results SS-STP		Mean	Results SS-STP
Depth of braincase					
8	7.38		4	7.38	
10	7.36		9	7.37	
13	7.35		8	7.32	
11	7.30		13	7.31	
4	7.28		6	7.20	
9	7.23		12	7.19	
12	7.21		10	7.19	
7	7.18		11	7.17	
6	7.08		7	7.15	
5	7.07		5	7.03	
1	6.80		2	6.66	
2	6.65		3	6.60	
3	6.60				

often have well-developed processes, whereas those from Tobago (5), Margarita Island (10), and northern Venezuela (11) usually have poorly-developed postpalatal processes.

Multivariate Analysis

The 16 external and cranial measurements, color, and nine qualitative cranial characters were analyzed using NT-SYS programs; distance and correlation matrices were computed and phenograms were generated to display phenetic relationships of both males and females of *Glossophaga longirostris*. Distance phenograms are presented herein because they have larger coefficients of cophenetic correlation (Fig. 15). Selected distance coefficients between (usually adjacent) samples for each sex also are included (Fig. 16).

Three clusters are evident in the distance phenogram for male *G. longirostris*. Specimens from the upper Magdalena Valley (8) are extremely large in external and cranial measurements and have well-developed postpalatal processes; those from Aruba (1) and Bonaire (3), although based on single individuals, are also large externally and cranially. The third cluster includes the remaining populations, the most distinctive of these being the relatively small specimens with modestly developed pterygoid alae from central Venezuela (12). Specimens from samples 2 (Curaçao) and 6 (Grenada) have narrow crania and group together, and those from sample 13 (Guyana) tend to be small in measurements of the wing and cranial length.

The distance phenogram for female *G. longirostris* also reveals three groups of clusters. The single specimen from Bonaire (3) is phenetically distinct in being

FIG. 15.—Distance phenograms for 13 samples of *Glossophaga longirostris*. Phenograms were computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages for males (left) and females (right). The cophenetic coefficient of correlation for the phenogram for males is 0.912 and for females is 0.843. See Figure 14 and text for key to samples.

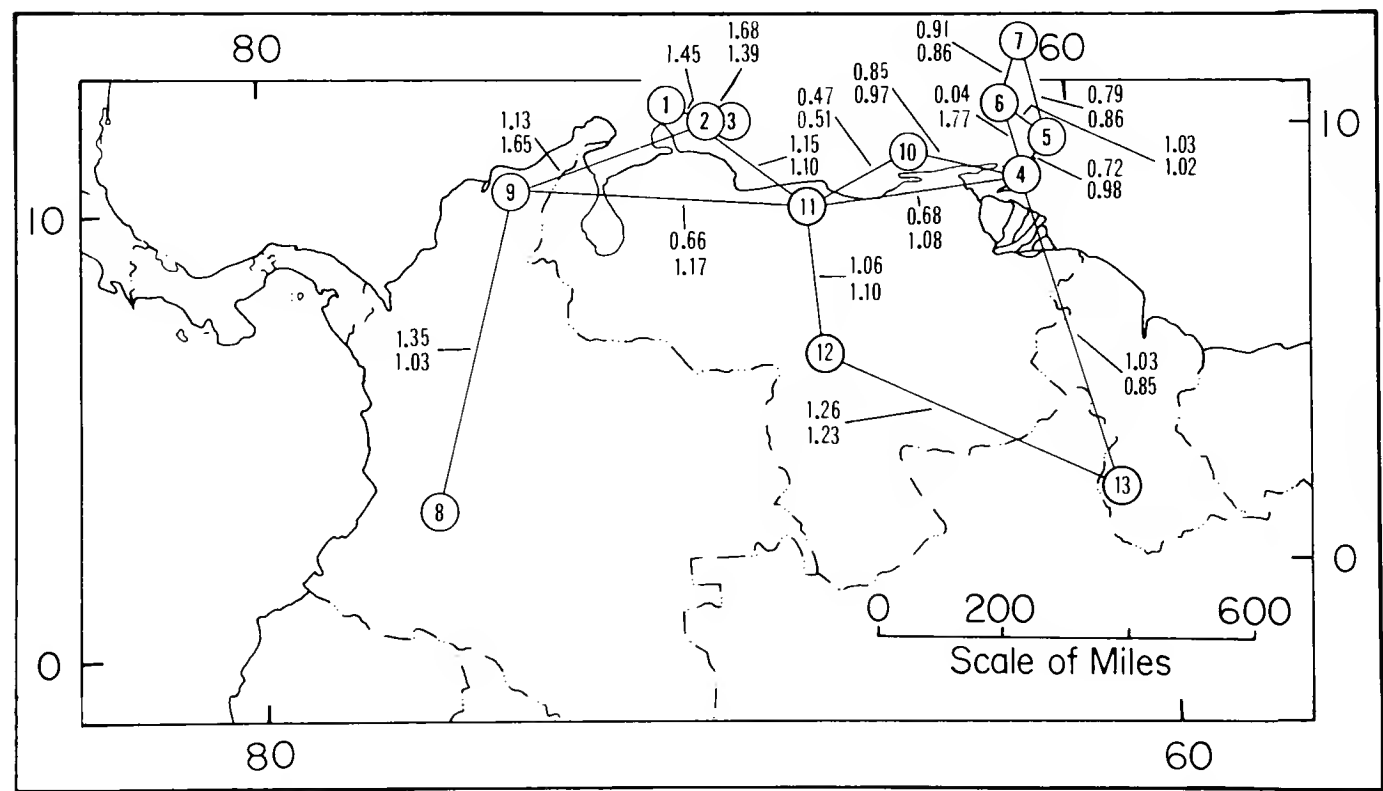
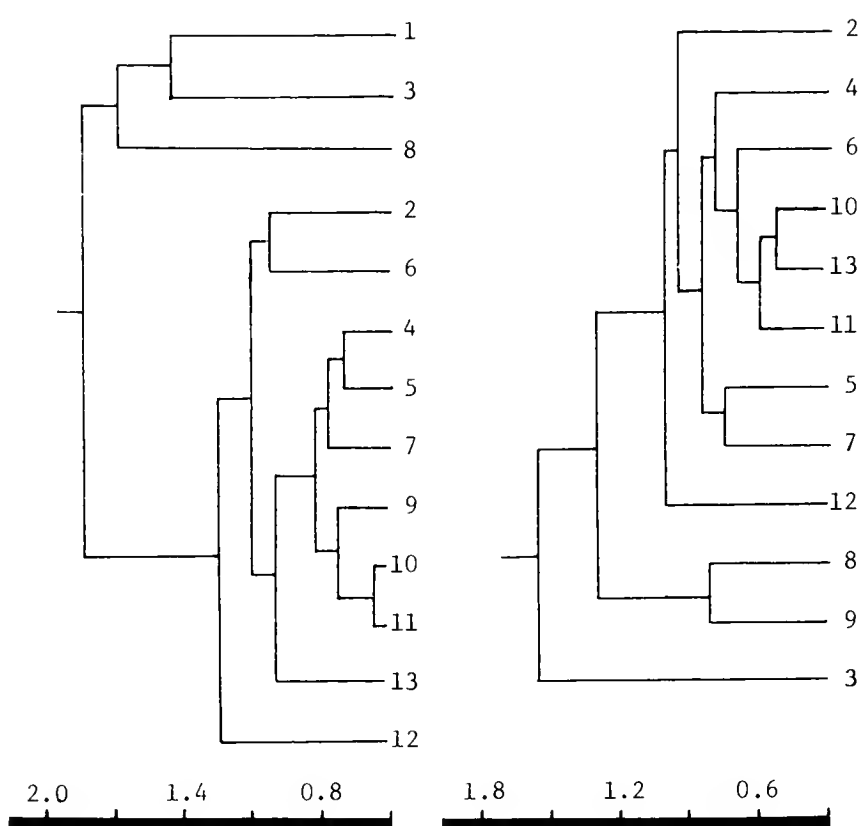
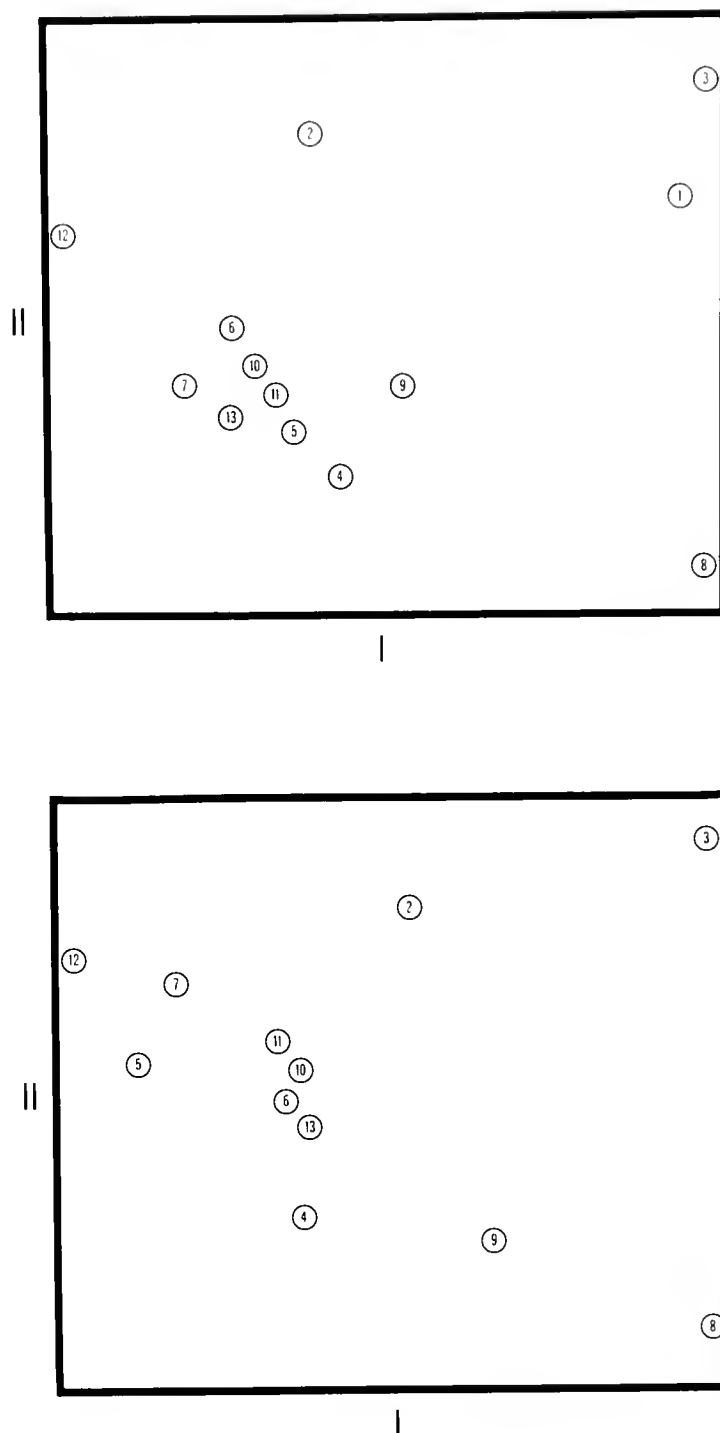


FIG. 16.—Selected distance coefficients among 13 samples of *Glossophaga longirostris*. Coefficients are from distance matrices for males (above) and females (below). See Figure 14 and text for key to samples.

smaller than average for the species in measurements of the wing and cranial breadth and in possessing well-developed postpalatal processes and a narrow P4. Specimens from samples 8 and 9 (Colombia and northwestern Venezuela) form the second cluster and are large in all measurements and have a more pronounced slope from rostrum to braincase. The remaining samples cluster together, the most diver-

FIG. 17.—Two-dimensional plots for 13 samples of *Glossophaga longirostris*. Component I plotted against component II for males (top) and females (bottom). See Figure 14 and text for key to samples.



gent being the one representing relatively small individuals with vestiges of pterygoid alae from central Venezuela (12), and specimens from Curaçao (2), which tend to be small in measurements of the wing and cranial width but large in measurements of cranial length.

The first four principal components were computed from the correlation matrix among the 26 characters of the 13 samples based on the matrix of correlation among characters for both males and females. The first four principal components combine to express 83.8 percent of the phenetic variation in males and 87.0 percent in females. The amount of phenetic variation represented in the first four principal components for males and females, respectively, was 42.4 and 40.0 for component I, 23.7 and 31.8 for component II, 9.4 and 9.4 for component III, and 8.3 and 5.8 for component IV. Two-dimensional plots of principal component I-II are presented

for both sexes (Fig. 17). Characters with loadings above 0.60 (or below -0.60) on the first four principal components are shown in Table 14.

The two-dimensional plots of male and female *G. longirostris* are similar. Samples from Aruba (1), Bonaire (3), and central Colombia (8) are on the right-hand side of component I and consist of bats that are larger than average for the species in measurements of cranial length. Sample 12 (central Venezuela) represents specimens that are smaller than average in these measurements, and, therefore, is located on the left-hand side of component I. OTUs to the top of component II are from the Netherlands Antilles (1-3), where specimens are narrower than average for the species in measurements of cranial width, whereas those to the bottom of component II contain individuals that are wider than average and include sample 8 (upper Magdalena Valley).

Taxonomic Conclusions

Patterns of geographic variation and a fragmented geographic distribution indicate that there are six recognizable subspecies of *Glossophaga longirostris*. Bats from Aruba, Curaçao, and Bonaire are characterized by small measurements of the wing, a moderately long cranium that is narrow throughout (particularly the rostrum and braincase), reduced postorbital swellings, and a flat facial profile. The trinomial *Glossophaga longirostris elongata* Miller, applies to these specimens from the Netherlands Antilles.

The apparently disjunct population of bats in the upper Magdalena River Valley, *Glossophaga longirostris reclusa* Webster and Handley, is distinguished by its massive size in external and cranial measurements, long and thick rostrum, long and deep braincase, and well-developed postpalatal processes. Individuals of this race resemble specimens from northern Colombia and northwestern Venezuela in that the postorbital swellings are reduced and the facial profile is slightly dished rather than flat (as in *G. l. elongata*) or moderately to noticeably dished (as in specimens from east and south of the Cordillera de Mérida).

Specimens from northern Colombia and northwestern Venezuela constitute another phenetically distinct race, *Glossophaga longirostris longirostris* Miller, and exhibit a gradual increase in size, both externally and cranially, from southwest to northeast. Individuals from Península de la Guajira (Colombia) and Península de Paraguaná (Venezuela) are the largest in this cline, those from Cartegena (Colombia) and Agua Santa (Venezuela) are smallest. This race is distinguished by a moderately large and low braincase, a long and thick rostrum, reduced postorbital swellings, and a slightly dished facial profile.

Another subspecies, *Glossophaga longirostris major* Goodwin, occurs along the xeric coast of Venezuela southward through the upper llanos of Colombia and Venezuela, and eastward to Trinidad. This race is characterized by a short and high braincase, noticeably dished facial profile, moderately long and narrow rostrum,

TABLE 14.—*Factor loadings for 26 characters examined in Glossophaga longirostris. Only loadings above 0.600 (or below -0.600) on the first four principal components are shown (males above, females below).*

Character	I	II	III	IV
Length of forearm	0.750			
		-0.915		
Length of third metacarpal	0.951			
		-0.724		
Length of fourth metacarpal	0.808			
		-0.898		
Length of fifth metacarpal	0.792			
		-0.866		
Greatest length of skull	0.943			
	0.970			
Condylobasal length	0.936			
	0.960			
Zygomatic breadth		-0.828		
		-0.902		
Length of rostrum	0.968			
	0.924			
Mastoid breadth		-0.891		
		-0.956		
Interorbital breadth		-0.671		
		-0.838		
Breadth of braincase		-0.809		
		-0.923		
Depth of braincase		-0.841		
		-0.879		
Length of maxillary toothrow	0.962			
	0.958			
Length of mandibular toothrow	0.955			
	0.913			
Width across molars	0.937			
	0.709			
Mandibular length	0.952			
	0.953			
Pelage coloration	-0.690			
	-0.637			
Pterygoid alae		0.873		
Presphenoid ridge		-0.728		
Lower incisors				
		-0.754		
Upper incisor angle			0.632	
	0.600			
Upper incisor size		-0.836		

TABLE 14.—Continued.

Character	I	II	III	IV
Basisphenoid			−0.685	
pits			0.889	
P3:P4 bulk			−0.800	
	0.838			
Slope of				
rostrum		−0.826		
Postpalatal				
processes	0.720			

and pronounced postorbital swellings. *G. l. major* is variable in cranial morphology throughout its geographic distribution, because of a cline in the doming of the braincase, and in measurements of the wing. Specimens from Trinidad and adjacent Venezuela have a high braincase and large wing measurements, whereas those to the west become progressively lower and smaller, respectively. Gene flow with other races to the west and south also contributes to geographic variation. Specimens from eastern Falcón (Venezuela), although most closely resembling *G. l. major*, exhibit intergradation with *G. l. longirostris* in that the braincase is long and low, the postorbital swellings are reduced, the rostrum is long and narrow, and the facial profile is less dished than those of individuals of *G. l. major* from north-eastern Venezuela.

Specimens from the llanos of Venezuela and surrounding the Kanuku Mountains at low elevations in Guyana and Brazil, *Glossophaga longirostris campestris* Webster and Handley, are highly variable in cranial morphology, but can be distinguished from other subspecies by their relatively small size in external and cranial dimensions, short and slender rostra, short and low braincases, moderately dished facial profiles, and moderately large postorbital swellings. Intergradation between this race and *G. l. major* is seen in specimens from southern Guárico as the rostrum becomes longer and the braincase becomes more globose; still these bats most closely resemble those from farther south.

The insular populations that are known from Tobago and the Windward Islands from Grenada northward to St. Vincent represent a phenetically distinct race, *Glossophaga longirostris rostrata* Miller, that is characterized by a narrow rostrum, moderately reduced postorbital swellings, a low and narrow braincase, a moderately dished facial profile, and zygoma that converge anteriorly. Specimens from Tobago are relatively larger in external and cranial dimensions and those from St. Vincent are relatively smaller, but the differences among the insular populations are not as great as between those from the islands and *G. l. major* of Trinidad and adjacent mainland.

Glossophaga longirostris campestris Webster and Handley

1986. *Glossophaga longirostris campestris* Webster and Handley, Occas. Papers Mus., Texas Tech Univ., 100:8, 18 March.

Holotype.—Adult female, skin and skull, USNM 389033, from Hato San José, 20 km. W Paragua (=146 km. S, 7 km. E Ciudad Bolívar), Venezuela, 300 m.; obtained on 8 April 1967 by members of the Smithsonian Venezuelan Project (N. Peterson, D. Peacock, and R. Peacock), original no. SVP 12679. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Total length, 72; length of tail, 8; length of hind foot, 12; length of ear from notch, 15; length of forearm (dry), 38.0; greatest length of skull, 22.3; condylobasal length, 21.2; zygomatic breadth, 9.6; mastoid breadth, 9.2; interorbital breadth, 4.4; length of maxillary toothrow, 7.6; length of mandibular toothrow (c-m3), 8.1; weight, 11.7 grams.

Distribution.—Llanos and Río Ventuari Basin of central Venezuela and surrounding the Kanuku Mountains in Guyana and adjacent Brazil (Fig. 18); known altitudinal distribution from 50 to 300 meters in elevation.

Comparisons.—A small subspecies of *Glossophaga longirostris*, both externally and cranially; variable in cranial proportions. The rostrum is usually short and narrow, the braincase is shallow and moderately low, the facial profile is moderately dished, and the postorbital swellings are moderately large.

Intergradation between *G. l. major* and *G. l. campestris* is evident in specimens from southern Guárico and northern Apure. The braincase of these bats is deeper and more bulbous (similar to *G. l. major*); however, these specimens agree with *G. l. campestris* in possessing short, narrow rostra and in small size overall.

Remarks.—Specimens of *G. l. campestris* have been collected from rock crevices, hollows of trees, and buildings. Pregnant females are known from December, and reproductively inactive females have been collected in April, June, and December.

Average external measurements (extremes in parentheses) of seven males, followed by those of seven females, of *G. longirostris campestris* are: total length, 66.6 (60-69), 68.3 (63-72); length of tail, 7.9 (6-9), 8.1 (7-9); length of hind foot, 12.0 (11-13), 11.7 (11-12); length of ear from notch, 15.6 (14-17), 15.0 (14-16).

Specimens examined (292).—BRAZIL. *Roraima*: Lucetania Ranch, 8 (ROM). GUYANA. *Rupununi*: Achimeriwau Mouth, 1 (ROM); "Bush Island," Dadanawa, 2 (AMNH); Chipirari Wau Mouth, 15 mi. E Dadanawa, 1 (ROM); Contanrib Island, 5 mi. above Dadanawa, 10 (ROM); 15 mi. ENE Dadanawa, 1 (ROM); 0-20 mi. E Dadanawa, 18 (2 AMNH, 16 ROM); Illia Wau River, 1 (ROM); Karanambo, 1 (AMNH); Kuitaro River, 5 (ROM); Mt. Tawatawun, ca. 8 km. E Dadanawa, 3 (ROM); Ruawau River, 30 mi. SW Dadanawa, 3 (ROM); Rock Cave, ca. Sand Creek Reservation, 5 (ROM); Sand Creek Village, 8 (ROM); "southern savannas," 17 (USNM); upper Sawariwau River, 7 (ROM); Wee Wee Tan, Makow Tan, 5 (ROM); Weri More, 4 (ROM). VENEZUELA. *Apure*: Hato Cariben, La Villa, 60 km. (=32 mi.) NE Puerto Páez, 76 m., 97 (USNM);

Hato "La Guanota," 6 km. W San Fernando de Apure, 100 m., 1 (TCWC); Río Cinaruco, 41 km. NW Puerto Páez, 24 (USNM); *ca.* 4 km. W San Fernando de Apure, 66 m., 2 (TCWC); San Rafael de Atamaica, 45 km. S, 6 km. E San Fernando de Apure, 100 m., 7 (USNM). *Bolívar*: Hato La Florida, 14 km. S, 45 km. E Caicara, 50 m., 10 (USNM); Hato San José, 20 km. W La Paragua (=146 km. S, 7 km. E Ciudad Bolívar), 300 m., 10 (USNM); Isla de Cuba (Playa del Medio), Río Orinoco, 3 (UCV); Paso Caruachi, Río Caroní, 3 (UCV). *T. F. Amazonas*: Chaparito, 9 km. SE Puerto Ayacucho, 119 m., 6 (USNM); Coromoto, 25 km. SSE Puerto Ayacucho, 126 m., 1 (USNM); Guayabal, 28 km. S Puerto Ayacucho, 135 m., 1 (USNM); Las Queseras, 12 km. SSE Puerto Ayacucho, 135 m., 4 (USNM); Morocoy, 65 km. SSW Puerto Ayacucho, 161 m., 3 (USNM); Pariá, 25 km. SSE Puerto Ayacucho, 114 m., 2 (USNM); Puerto Ayacucho, 2 (UCV); 0.75 km. E San Juan, Río Manapiare, 1 (USNM); *ca.* 4 km. W San Juan, Río Manapiare, *ca.* 163 km. ESE Puerto Ayacucho, *ca.* 155 m., 13 (USNM); Tamanaco, 4 km. NE San Juan, Río Manapiare, 155 m., 2 (USNM).

Additional records.—VENEZUELA. *Apure*: Hato "El Frio" (Ibañez U., 1984).

Marginal records.—VENEZUELA. *Apure*: Hato "La Guanota," 6 km. W San Fernando de Apure, 100 m. *Bolívar*: Paso Caruachi, Río Caroní; Hato San José, 20 km. W La Paragua (=146 km. S, 7 km. E Ciudad Bolívar), 300 m. *T. F. Amazonas*: *ca.* 4 km. W San Juan, Río Manapiare, *ca.* 163 km. ESE Puerto Ayacucho, *ca.* 155 m. GUYANA. *Rupununi*: Karanambo; Rauwau River, 30 mi. SE Dadanawa. BRAZIL. *Roraima*: Lucetania Ranch.

Glossophaga longirostris elongata Miller

1900a. *Glossophaga elongata* Miller, Proc. Biol. Soc. Washington, 13:124, 6 April.

1958. *Glossophaga longirostris elongata*, Koopman, Evolution, 12:437, December.

Holotype.—Adult female, skin (from a specimen in alcohol) and skull, USNM 101871, from Willemstad, Curaçao; obtained on 4 December 1899 by J. L. Guthrie, no original number. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Total length, 65; length of tail, 5.5; length of hind foot (dry), 11.4 (Miller, 1900a); length of ear from meatus, 14.6 (Miller, 1900a); length of forearm (dry), 38.9; greatest length of skull, 24.6; condylobasal length, 22.6; zygomatic breadth, 9.4; mastoid breadth, 9.2; interorbital breadth, 4.4; length of maxillary toothrow, 8.4; length of mandibular toothrow (c-m3), 8.8.

Distribution.—Aruba, Curaçao, and Bonaire (Fig. 18).

Comparisons.—An insular subspecies that is characterized by small measurements of the wing, an extremely narrow but moderately long cranium, and an exceedingly low braincase. The postorbital swellings are reduced and the facial profile is flat or slightly arched rather than noticeably dished as in other races of *G. longirostris*. In addition, the zygoma of *G. l. elongata* are swept back in linear fashion rather than being flared as in specimens from the adjacent mainland.

Remarks.—Bats from the three Dutch islands exhibit variation in cranial dimensions, but the differences among them (based on small samples from Aruba and Bonaire) are not as great as between the islands and the mainland. Island and mainland populations are not so different, however, that occasional specimens are indistinguishable. The holotype of *G. l. elongata* is the largest of the series from

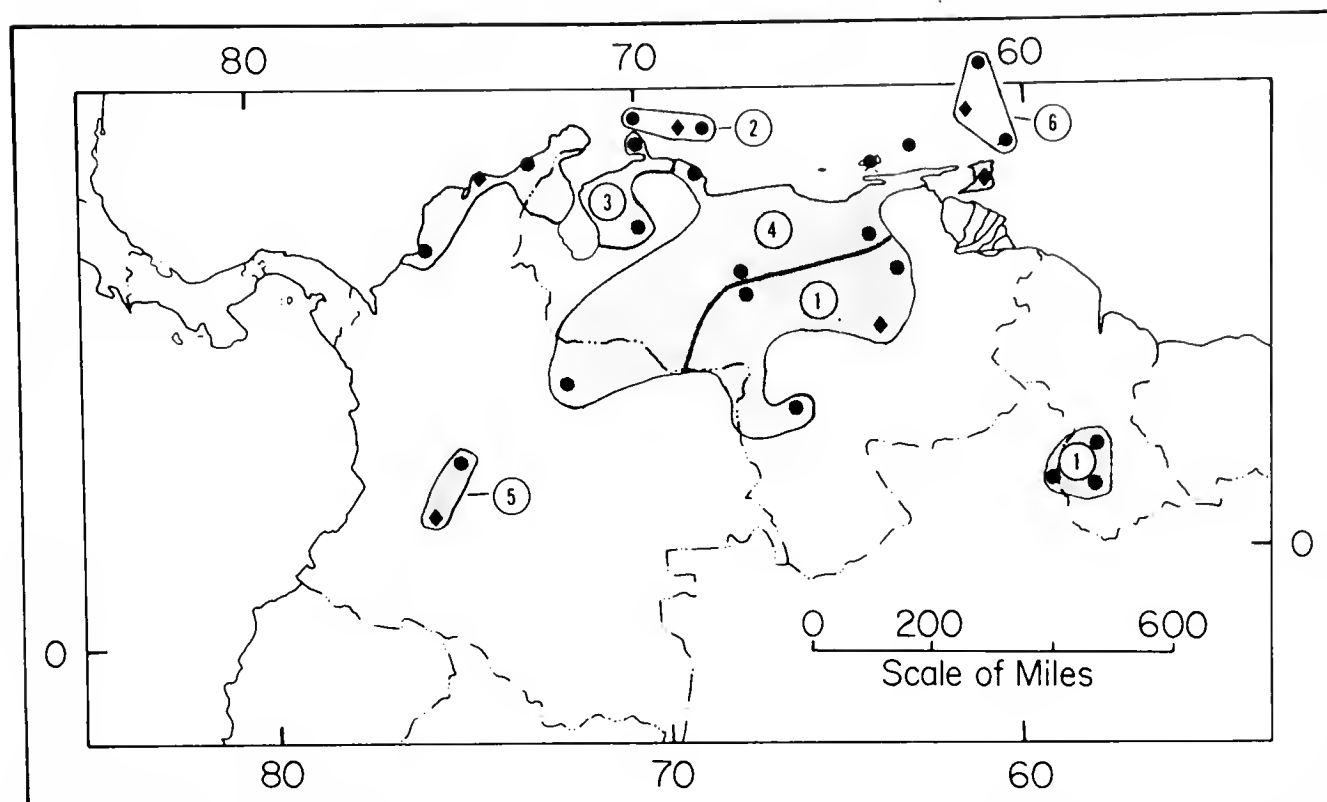


FIG. 18.—Geographic distribution of six recognized subspecies of *Glossophaga longirostris* in South America. Recognized races are *G. l. campestris* (1), *G. l. elongata* (2), *G. l. longirostris* (3), *G. l. major* (4), *G. l. reclusa* (5), and *G. l. rostrata* (6). Circles represent marginal localities and diamonds represent type localities.

Curaçao, and its flat facial profile does not resemble that of any individual I have examined from the mainland.

Some individuals have been collected from caves and rock fissures and others have been taken in mist nets set over water (Genoways and Williams, 1979a; Miller, 1900b). Nine females collected in February evinced no reproductive activity; however, volant young, subadult, and adult specimens were collected in August, indicating the recent termination of a reproductive cycle (Genoways and Williams, 1979a).

Average external measurements (extremes in parentheses) of four males, followed by those of five females, of *G. l. elongata* are: total length, 59.8 (52-65), 65.8 (58-74); length of tail, 2.3 (0-5), 3.9 (0-5.5); length of hind foot, 11.0 (10-12); 11.0 (11); length of ear from notch, 12.0 (11-13), 12.3 (11-14).

Specimens examined (42).—NETHERLANDS ANTILLES. *Aruba*: Quaridikiri Cave, 1 (AMNH); no locality, 4 (USNM). *Bonaire*: Bolivia Dist., 2 (AMNH); no locality, 1 (USNM). *Curaçao*: NW end of island, 6 (USNM); Round Cliff, 1 (AMNH); Savonet, NW Willemstad, 10 (5 AMNH, 5 USNM); SW side of island, 3 (USNM); Willemstad, 8 (USNM); no locality, 6 (2 AMNH, 1 FMNH, 3 USNM).

Additional records.—NETHERLANDS ANTILLES (Husson, 1960, unless otherwise noted). *Aruba*: Baranca Corá; Bubali; cave near Fontein (Hummelinck, 1940); Goudmijnschacht bij Bashiri; Santa Cruz; Seroe Canachito (Hummelinck, 1940); Zuster-Klooster, Noord. *Bonaire*: Cueba Watapana, Lima (Hummelinck, 1940); grot van Montagne, bij Dos Pos; huizen in Kralendijk; Spelonk. *Curaçao*: Bottelier; cave of Hato (Hummelinck, 1940); cave near Hermanus (Hummelinck, 1940); Cueba di Jelje, bij Hato; Cueba di Raton; grotten op Noordkant; Klein St.

Martha; landhuis Cas Abau; Mal Paies (Wille, 1954); Playa Hundu; Quarataine gebouw en Fort Beekburg bij Caracas-baai; 2.8 km. S, 4.5 km. E Westpunt (Genoways and Williams, 1979a).

Marginal records.—NETHERLANDS ANTILLES. *Aruba. Curaçao. Bonaire.*

Glossophaga longirostris longirostris Miller

1898. *Glossophaga longirostris* Miller, Proc. Acad. Nat. Sci. Philadelphia, 50:330, 25 July.

Holotype.—Adult female, skin and skull, MCZ 8046 (Bangs' Collection), from Santa Marta Mountains (near Santa Marta), Magdalena, Colombia; obtained on 10 February 1898 by W. W. Brown, Jr., original no. 60. Holotype examined; skin and skull in excellent condition except upper and lower incisors absent.

Measurements of the holotype.—Total length, 80; length of tail, 18; length of hind foot, 10; length of ear from notch, 14; length of forearm (dry), 39.5; condylobasal length, 21.8; zygomatic breadth, 10.2; mastoid breadth, 9.8; interorbital breadth, 4.3; length of maxillary toothrow, 8.1; length of mandibular toothrow (c-m3), 8.4.

Distribution.—Northern Colombia and northwestern Venezuela (Fig. 18); known altitudinal distribution from sea level to approximately 615 meters in elevation.

Comparisons.—A moderately large race of *G. longirostris* that is characterized by a long, stout rostrum, long and low braincase, reduced postorbital swellings, and a moderately flat facial profile. An increase in size in external and cranial dimensions from southwest to northwest is evident; specimens from Península de la Guajira and Península de Paraguaná are the largest in this cline and approach *G. l. reclusa* in overall size. However, *G. l. longirostris* can be distinguished from *G. l. reclusa* by its less globose and lower braincase, and the postpalatal processes are poorly developed and not falcate.

Remarks.—Known daytime roosts include caves (J. A. Allen, 1900). Specimens have been collected in mist nets near farm buildings and in gallery forest (Pirlot, 1964). Pregnant and lactating females have been collected in June in Venezuela. Specimens in the process of molt also have been collected in June.

Albuja (1983), in his opus on Ecuadorian bats, reported *G. l. longirostris* from Hda. El Timbre, Esmeraldas, and Río Palenque along the Pacific coast of that country. I have not included these localities in Figure 18 because photographs (Albuja, 1983:83) of the cranium and lower jaw of one specimen clearly indicate it is assignable to *G. soricina*, comments (Albuja, 1983:84) about the smaller noseleaf in individuals of *G. longirostris* (as compared to that in individuals of *G. soricina*) are incorrect (see Webster and Handley, 1986), and measurements attributable to the specimens in question were compared with those of *G. s. soricina*, which is distinctly smaller and occurs east of the Andes, and not with those of the sympatric *G.*

s. valens, which is similar to *G. longirostris* in many external and cranial dimensions.

Average external measurements (extremes in parentheses) of nine males, followed by those of five females, of *G. l. longirostris* are: total length, 68.9 (61-72), 72.6 (69-80); length of 6.6 (5-9), 7.7 (4-18); length of hind foot, 12.8 (12-14), 12.8 (10-14); length of ear from notch, 16.7 (16-17), 16.1 (14-17).

Specimens examined (296).—COLOMBIA. *Atlántico*: Barranquilla, 1 (FMNH); La Playa, 2 (AMNH). *Bolívar*: Bahía de Cartagena, Fuerte de San Fernando, 2 (FMNH); Cartagena, 2 (USNM). *Guajira*: 114-121 km. N, 25-32 km. W Maracaibo (Venezuela), 15-50 m., 27 (USNM); Valledupar (=Magdalena), Villanueva, 274 m., 5 (USNM). *Magdalena*: Bonda, 50 m., 5 (4 AMNH, 1 USNM); Mamatoco, Santa Marca [Marta], 15 m., 3 (CMNH); Minca, 600 m., 1 (USNM); Santa Marta Mountains (near Santa Marta), 1 (MCZ); Taganga, 0 m., 29 (26 AMNH, 2 CMNH, 1 USNM). *Sucre* (=Bolívar): Tolúviejo, 1 (USNM). VENEZUELA. *Falcón*: Cabo San Román, Península de Paraguaná, 1 (UCV); Capatárida, 40 m., 116 (USNM); 48-49 km. N, 33-46 km. W Coro, Península de Paraguaná, 13-615 m., 36 (USNM); 20 km. S, 98 km. E Maracaibo, Hda. Socopito, 480 m., 1 (USNM); Río Tocuyo, 500 m., 5 (AMNH). *Lara*: 10 km. N El Tocuyo, Caserio Boro, 5 (USNM). *Trujillo*: 23 km. NW Valera, 90-95 m., 12 (USNM). *Zulia*: Maracaibo, 1 (FMNH); 110-114 km. N, 25-28 km. W Maracaibo, 5-15 m., 40 (USNM).

Additional records.—COLOMBIA (Morales-Alarcón *et al.*, 1968). *Guajira*: Maicao; Riohacha. VENEZUELA. *Lara*: Guárico (J. A. Allen, 1911). *Zulia*: Hda. El Cerro, ca. Rosario, Rio Palmar (Pirlot, 1964).

Marginal records.—COLOMBIA. *Bolívar*: Tolúviejo. *Guajira*: Maicao. VENEZUELA. *Falcón*: Cabo San Román, Península de Paraguaná. *Lara*: 10 km. N El Tocuyo, Caserio Boro.

Glossophaga longirostris major Goodwin

1958. *Glossophaga major* Goodwin, Amer. Mus. Novit., 1877:5, 28 February.

1958. *Glossophaga longirostris major*, Koopman, Evolution 12:438, December.

Holotype.—Adult female, skin and skull, AMNH 176288, from Ariapita Avenue, Woodbrook, Port of Spain, Trinidad; obtained on 13 June 1957 by M. Sookar, original no. 57-1200. Holotype examined; skin prepared from fluid preserved specimen, and skull badly broken, partially repaired with glue (Webster and Handley, 1986).

Measurements of the holotype.—Total length, 61; length of tail, 7; length of hind foot, 11.5; length of ear from notch, 20; length of forearm (dry), 41.9; length of maxillary toothrow, 8.3; length of mandibular toothrow (c-m3), 8.7.

Distribution.—Northern Venezuela southward through the upper llanos of Venezuela and Colombia, and eastward to Trinidad (Fig. 18); known altitudinal distribution from sea level to approximately 305 meters in elevation.

Comparisons.—A medium-sized race of *G. longirostris* that is unusually variable in external measurements and cranial morphology; distinguished from other races by its short and high braincase, pronounced postorbital swellings, long and narrow rostrum, and noticeably dished facial profile. Variability is due, in part, to a

cline in the length of wing bones and the depth of braincase; specimens from eastern Venezuela and Trinidad have large external measurements and an extremely high braincase, but bats to the west become smaller and shallower, respectively, in these dimensions.

Intergradation also contributes to the variability exhibited in *G. l. major*. Gene flow with *G. l. longirostris* is evident in populations from Boca de Yaracuy and Mirimire. In these specimens the postorbital swellings are reduced, the facial profile is less abrupt, and the cranium is longer, but in other respects they agree with *G. l. major*.

Remarks.—Known daytime roosts frequented by *G. l. major* include caves, houses, and buildings. It was found roosting with *Glossophaga soricina* at San Julián, Venezuela (Robinson and Lyon, 1901), and has been captured in mist nets in peach and mango orchards (Smith and Genoways, 1974).

Pregnant females have been collected in January, February, March, April, July, and August; lactating females are known from January, June, September, October, and December. Individuals in the process of molt have been collected in July, October, and November.

Pirlot (1965) recorded *G. longirostris* from Guayo, T. F. Delta Amacuro, Venezuela, but this locality is not included in Figure 18 because the xeric environments preferred by this bat are not found in that territory (Webster and Handley, 1986).

Average external measurements (extremes in parentheses) of 21 males, followed by those of 22 females, of *G. l. major* are: total length 68.3 (62-75), 68.8 (60-76); length of tail, 6.9 (4-12), 7.3 (4-12); length of hind foot, 11.6 (9-15), 11.4 (10-13); length of ear from notch, 15.6 (11-18), 16.9 (14-20).

Specimens examined (374).—COLOMBIA. *Casanare* (=Boyacá): Pore, 1 (USNM). TRINIDAD. *St. George*: Gasparee Island, Gasparee Caves, 1 (OU); Port of Spain, 23 (14 AMNH, 1 LACM, 6 UMMZ, 2 USNM). *No locality*: 7 (1 FMNH, 6 UMMZ). VENEZUELA. *Anzoátegui*: Cantuara, 1 (USNM). *Aragua*: 1 km. S Ocumare de la Costa, 2 (USNM). *Carabobo*: San Esteban, 8 (AMNH). *Cojedes*: Galeras del Pao, 1 (UCV). *Distrito Federal*: Chichirivichi, 2 (UCV); La Guaira, 1 (USNM); Macuto, 3 mi. E La Guaira, 22 (2 AMNH, 1 FMNH, 1 MVZ, 18 USNM); Peña de Mora, 2 (USNM); San Julián, 8 mi. E La Guaira, 8 (1 MCZ, 7 USNM). *Falcón*: ca. Agüide, 19 km. N, 4 km. E Mirimire, 1-5 m., 20 (USNM); border with *Carabobo*, Boca de Yaracuy, 35 km. NW Puerto Cabello, 2 m., 14 (USNM). *Guárico*: Altagracia (de Orituco), 2 (FMNH); Calabozo, 100 m., 13 (USNM); Embalse de Guárico, 10 km. N Calabozo, 100 m., 19 (USNM); Estación Biológica de los Llanos, 12 km. S, 7 km. E Calabozo, 100 m., 1 (USNM); Hato Las Palmitas, 34 km. S, 12 km. W San Juan de los Morres, 181 m., 2 (USNM); Hato Masaguaral, 8 km. N, 2 km. W Corozo Pando, 100 m., 1 (TCWC); San Jose de Tiznados, 76 km. N, 16 km. W Calabozo, 150 m., 69 (USNM). *Miranda*: Hda. Bejuquero, S Río Chico, 1 m., 14 (USNM); 7 km. N Río Chico, 2 (USNM); 5 km. W Río Chico, ca. Puerto Tuy, sea level, 6 (USNM). *Nueva Esparta*: Cerro Matasiete, 2 km. N, 1 km. E La Asunción, 305 m., 32 (USNM); El Valle, 50 m., 7 (KU); ca. La Aguada, 3 km. S La Asunción, 53 m., 32 (USNM); 1 km. E La Guardia, 18 m., 1 (USNM); La Vencindad, 4 km. N, 8 km. W La Asunción, 19 m., 2 (USNM); Salamanca, 2 km. N, 1 km. E La Asunción, 38 m., 16 (USNM); 0.5 km. N San Francisco de Macanao, 75 m., 2 (KU); ca. Teatas de María Guevara, 2 km.

N, 30 km. W Porlamar, 10 m., 1 (USNM). *Sucre*: 0-2.5 km. SE Cumaná, 10 m., 11 (KU); Ensenada Cauranta, 7 km. N, 5 km. E Güiria, 4 m., 4 (USNM); Isla de los Patos, 6 (2 AMNH, 1 FMNH, 3 MVZ); Quetepe, 16 km. E Cumaná, sea level, 7 (USNM); 5 km. E San Antonio del Golfo, 1 (KU); ca. Sotillo, 21 km. E Cumaná, 30 m., 10 (USNM).

Additional records.—TRINIDAD. *St. Patrick*: Point Fortin (Goodwin and Greenhall, 1961). VENEZUELA. *Aragua*: Cueva de Quebrada Honda (as *G. soricina*) (Linares, 1968). *Nueva Esparta*: Islas los Testugos, Isla de Conejo (Hummelinck, 1940).

Marginal records.—VENEZUELA. *Falcón*: Agüide, 19 km. N, 4 km. E Mirimire, 1-5 m. *Nueva Esparta*: Isla de Margarita; Islas los Testugos. *Anzoátegui*: Cantaura. *Guárico*: Hato Masaguaral, 8 km. N, 2 km. W Coroza Pando. COLOMBIA. *Casanare* (=Boyacá): Pore. TRINIDAD.

Glossophaga longirostris reclusa Webster and Handley

1986. *Glossophaga longirostris reclusa* Webster and Handley, Occas. Papers Mus., Texas Tech Univ., 100:14, 18 March.

Holotype.—Adult female, skin and skull, MVZ 113903, from 4 km. E Villavieja, Huila, Colombia, 1400 ft.; obtained on 1 July 1950 by O. P. Pearson, original no. 3082. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Head and body length, 66; [length of tail, 0;] length of hind foot (dry), 13; length of ear from notch, 15; length of forearm (dry), 41.2; greatest length of skull, 24.0; condylobasal length, 22.5; zygomatic breadth, 10.0; mastoid breadth, 9.6; interorbital breadth, 4.4; length of maxillary toothrow, 8.5; length of mandibular toothrow (c-m3), 9.0; weight, 13 grams.

Distribution.—Upper Magdalena Valley of Colombia at least from Cundinamarca southward to Huila (Fig. 18); known altitudinal distribution from approximately 325 to 500 meters in elevation.

Comparisons.—A large subspecies of *Glossophaga longirostris*, both externally and cranially. The braincase is more globose and the postpalatal processes are well developed and more falcate than those of the other races. *G. l. reclusa* and *G. l. longirostris* are similar in several cranial dimensions that separate them from the other subspecies; their rostra are long and stout rather than shorter or slenderer (or both), their postorbital swellings are reduced in size, and the break in their facial profiles (lateral view) is less obvious than that in bats from populations to the east and south of the Cordillera de Mérida, but more dished than that of *G. l. elongata*. The dorsal pelage of *G. l. reclusa*, although bicolored and variable in coloration as in other taxa of *Glossophaga*, averages greater in contrast between the brownish tips and paler bases of the individual hairs than in other races of *G. longirostris*, and is similar to that of *G. morenoi mexicana* of southern México (Webster and Jones, 1980).

Remarks.—*G. l. reclusa* and *G. l. longirostris* are similar in cranial morphology and are distinguished primarily by differences in external and cranial measurements; the former exceeds the latter in most. However, if *Glossophaga longirostris* is continuously distributed in the Magdalena Valley, then specimens from southern Bolívar, western Norte de Santander and Santander, and eastern Antioquia may be

intermediate in size and a cline in body proportions may exist. I have not examined individuals that demonstrate gene flow between these races, but specimens have been reported from Santander (Morales-Alarcón *et al.*, 1968); these and other individuals from the Magdalena Valley should be compared to better define the relationships between these two taxa.

Specimens of *G. l. reclusa* have been collected from culverts and small caves in the hot, semiarid Magdalena River Valley. They were found roosting with *Micronycteris megalotis* in a culvert near Villavieja, and have been captured in the same mist net as *Glossophaga soricina* at Giradot (Tamsitt and Valdivieso, 1963; Valdivieso, 1964).

Pregnant females have been collected in June and July and a lactating female was taken in June. Two females captured in November evinced no reproductive activity. Specimens in the process of molt have been collected in November.

Although the holotype was recorded as not having a tail, the sheath-like portion of the uropatagium that encloses the caudal vertebrae is clearly visible in that specimen, and the tail length averages 6.7 (range 4-10) in six other specimens from the vicinity of the type locality. Average external measurements (extremes in parentheses) of nine males, followed by those of 13 females, of *G. l. reclusa* are: total length, 66.1 (62-72), 69.9 (64-77); length of tail, 0.4 (0-4), 2.9 (0-10); length of hind foot, 12.2 (12-13), 12.1 (10-13); length of ear from notch, 15.7 (15-16), 15.7 (15-16).

Records of *G. longirostris* from two localities in the upper Magdalena Valley of Cundinamarca (Mesitas del Colegio) and Tolima (Mariquita), as well as another in Meta (Villavicencio) on the eastern Andean slope, by Valdivieso and Tamsitt (1962) were not referred to in subsequent publications by the same authors (Tamsitt and Valdivieso, 1963; Valdivieso, 1964), and therefore are not included in Figure 18.

Specimens examined (25).—COLOMBIA. *Cundinamarca*: 1 km. NE Giradot, 3 (AMNH). *Huila*: 5 km. N Villavieja, 1400 ft., 4 (MVZ); 4-7.5 km. E Villavieja, 1400 ft., 15 (MVZ); 17.5 km. SE Villavieja, 1600 ft., 3 (MVZ).

Marginal records.—COLOMBIA. *Tolima*: Mariquita, 233 m. *Huila*: 17.5 km. SE Villavieja, 1600 ft.

***Glossophaga longirostris rostrata* Miller**

1913a. *Glossophaga rostrata* Miller, Proc. Biol. Soc. Washington, 26:32, 8 February.

1913b. *Glossophaga longirostris rostrata*, Miller, Proc. U.S. Nat. Mus., 46:423, 31 December.

Holotype.—Presumably an adult female skull (see Handley and Webster, 1987, and remarks beyond), USNM 111500, from Westerhall Estate, Grenada; date of collection unknown, obtained by P. Gellineau, original no. 29. Holotype examined; skull in excellent condition.

Measurements of the holotype.—Greatest length of skull, 22.8; condylobasal length, 21.3; zygomatic breadth, 9.8; mastoid breadth, 9.5; interorbital breadth, 4.2; length of maxillary toothrow, 8.0; length of mandibular toothrow (c-m3), 8.5.

Distribution.—Lesser Antilles from St. Vincent southward to Grenada (except Barbados), and Tobago (Fig. 18); known altitudinal distribution from sea level to approximately 625 meters in elevation.

Comparisons.—Moderate in size in external and cranial dimensions relative to other races of *G. longirostris*; larger overall on Tobago, smaller on St. Vincent. The rostrum is narrow and the postorbital swellings are moderately reduced. The braincase is clearly less bulbous than that of *G. l. major* from Trinidad and northeastern Venezuela. The facial profile is moderately dished and zygoma converge anteriorly.

Remarks.—Handley and Webster (1987) opined that the holotype, selected by Miller from among 14 specimens collected by P. Gellineau on Grenada in 1900, consists of a mismatched skin (a male) and skull (a female). They, therefore, restricted the holotype designation to the female skull, the male skin becoming a paratype. Furthermore, they noted that the purported date of collection ("1900") was the date that Gellineau mailed the specimens to the USNM, not the actual date of collection.

Specimens of *G. l. rostrata* have been collected from hollow trees on Grenada. They were found roosting with *Peropteryx macrotis*, *Micronycteris megalotis*, *Phyllostomus hastatus*, and *Carollia perspicillata* on Tobago (Goodwin and Greenhall, 1961). Pregnant females have been captured in August and December, and lactating females are known from March, June, and August. Individuals in the process of molt have been collected in August and September.

Average external measurements (extremes in parentheses) of seven males, followed by those of 14 females, of *G. l. rostrata* are: total length, 65.7 (63-69), 68.1 (63-74); length of tail, 6.6 (5-11), 7.1 (5-11); length of hind foot, 10.9 (5-13), 12.1 (8.5-14); length of ear from notch, 14.6 (13-15), 15.4 (14-16).

Specimens examined (147).—LESSER ANTILLES. *Grenada*: Grand Etang, 2000 ft., 5 (1 AMNH, 4 MCZ); Grenville Vale, 5 (AMNH); Pointe Saline, 3 (AMNH); 0-3.5 mi. NE St. George, 16 (6 KU, 9 MCZ, 1 TTU); St. Pauls, 4 (TTU); True Blue, 3 (AMNH); 0.5 mi. E Vendome, 1000 ft., 7 (1 KU, 6 TTU); Westerhall Estate, 14 (USNM); no locality, 7 (ROM). *Grenadines*: Carriacou, 23 (17 MCZ, 6 TTU); Union Island, 1 (MCZ). *St. Vincent*: Brighton, 8 (AMNH); Clifton Hill, 400 ft., 22 (KU); Grand Sable Estate, 7 (MCZ); Mesopatamia, 300 ft., 2 (KU); no locality, 2 (ROM). *TOBAGO*. *Little Tobago*: 2 (AMNH). *St. Andrews*: Orange Hill Rd., 3 (AMNH); Scarborough Government House, 3 (AMNH). *St. David*: Grafton, ca. Plymouth, 1 (LSU). *St. John*: 1 km. N Speyside, 5 (USNM). *St. Mary*: Pembroke, Gold Borough Estate, 1 (AMNH). *St. Patrick*: 1 km. SW Crown Point Airport, 3 (USNM).

Additional records.—LESSER ANTILLES. *Grenada*: Grenada (Webster and Handley, 1986); Richmond Hill (G. M. Allen, 1911). *Grenadines*: Mustique (Webster and Handley, 1986). *TOBAGO*. Auchenskeoch (Husson, 1954).

Marginal records.—LESSER ANTILLES. St. Vincent. Grenadines. Grenada. TOBAGO.

Glossophaga morenoi
Moreno's Long-tongued Bat

Moreno's long-tongued bat is known currently only from southern México (Michoacán, Morelos, Puebla, Guerrero, Oaxaca, and Chiapas). This species is represented by an unsexed specimen (USNM 6992) from Tehuantepec, collected in February 1862, that provides the oldest record of an individual of *Glossophaga* examined during the course of this investigation. Although not included by Miller (1913*b*) in his revision of the genus, this specimen remained disguised as *Glossophaga soricina* for decades, in part due to a severely damaged skull and also to the composite nature of Mexican *G. soricina* prior to the recognition of sibling species in that geographic region.

Diagnosis

Size medium to large in measurements that reflect cranial length, medium in measurements of the wing and cranial breadth; upper incisors noticeably procumbent, I1 usually larger than I2 in bulk; fourth upper premolar relatively narrow, posterolingual cingular shelf not noticeably developed; parastyle of M1 reduced; parastyle of M2 directed labially from paracone, forming a well-developed notch between the parastyle and mesostyle; metastyle and fourth commissure of M1 and M2 elongate; lower incisors reduced in size, subcircular in occlusal view, with small gaps between the teeth, i1 usually smaller than i2 in bulk; premaxillae noticeably elongate; pterygoid alae absent or greatly reduced; presphenoid ridge flattened subterminally; mandibular symphyseal ridge reduced; pelage distinctly bicolored, the individual hairs having pale bases and darker tips, hair on the venter conspicuously frosted; color Rood's Brown to Clove Brown dorsally, Pale Drab Gray to Avellaneous ventrally; weight averaging 8.4 (7.3-9.2) in males and 8.6 (7.8-9.7) in nonparous females from throughout the range.

Comparisons

Means by which *Glossophaga morenoi* can be distinguished from *G. commisaris*, *G. leachii*, and *G. longirostris* are given in those accounts. *Glossophaga morenoi* can be distinguished from *G. soricina* by the relatively narrow P4 (distinct posterolingual cingular shelf in *G. soricina*), labially directed parastyle of M2 that forms a conspicuous notch with the mesostyle (parastyle of M2 directed antero-labially with no distinct notch in *G. soricina*), reduced lower incisors with gaps between the teeth (large and in contact in *G. soricina*), reduced mandibular symphyseal ridge (well developed in *G. soricina*), absent or poorly developed pterygoid alae (well developed in *G. soricina*), and a subterminally flattened presphenoid ridge (high and complete throughout in *G. soricina*).

Ecology and Reproduction

Little is known concerning the natural history of this long-tongued bat, which was not recognized by most mammalogists as a distinct species until 1980; however, it is a denizen of the relatively arid pine-oak forests of the Sierra Volcanica Transversal and Sierra Madre del Sur, and xeric thorn-scrub forests in the Isthmus of Tehuantepec (Webster and Jones, 1985). Daytime roosts include caves, hollow trees, road culverts, wells, and walls of buildings, but most specimens have been taken in mist nets set over rivers and creeks (Webster and Jones, 1980, 1985). I found *G. morenoi* relatively common in western Chiapas near Tonalá, where it was captured in mist nets set over the Río Ocuilapa in a habitat characterized as having a broken upper canopy of broadleaf trees and a dense lower canopy of other woody vegetation; there were few shrubs and scant ground vegetation. The surrounding rocky slopes supported mesquite, grasses, and cacti. Other species of bats taken at that place are listed in the account of *G. leachii*. Those taken with *G. morenoi* at Cañon de Zopilote in Guerrero (Winkelmann, 1962) included *Balaniopteryx plicata*, *Macrotus waterhousii*, *Musonycteris harrisoni*, *Desmodus rotundus*, and *Lasiurus intermedius*.

Of females collected in February (one), March (two), April (two), May (two), June (one), August (one), November (one), and December (one), one in March and one in November were pregnant and one each in the months of May, June, and December was lactating. Testes length averaged 4.0 (3.8-4.2) in four males taken in June and measured 8 by 6 in one male collected in July. This species is monotocous, but the extent of the reproductive season is poorly known (Webster and Jones, 1985).

Geographic Variation

Specimens from throughout the geographic range of *G. morenoi* were grouped into two samples (Fig. 19) as follows: *sample 1*—MICOACAN, MORELOS, and PUEBLA; *sample 2*—OAXACA and CHIAPAS. Standard statistics for both samples are given in Table 15. Because only two samples were analyzed, only univariate analyses were performed.

External measurements.—Specimens from Oaxaca and Chiapas (2) average larger than those from Michoacán, Morelos, and Puebla (1). Wing measurements are not significantly different between males in the two samples, but length of forearm and length of fifth metacarpal are significantly different between samples of females.

Cranial measurements.—Specimens from sample 2 (Oaxaca and Chiapas) average larger than those from sample 1 (Michoacán, Morelos, and Puebla) in all cranial measurements examined. Several measurements (greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, length of rostrum, length of maxillary toothrow, length of mandibular toothrow, and mandibular length) are

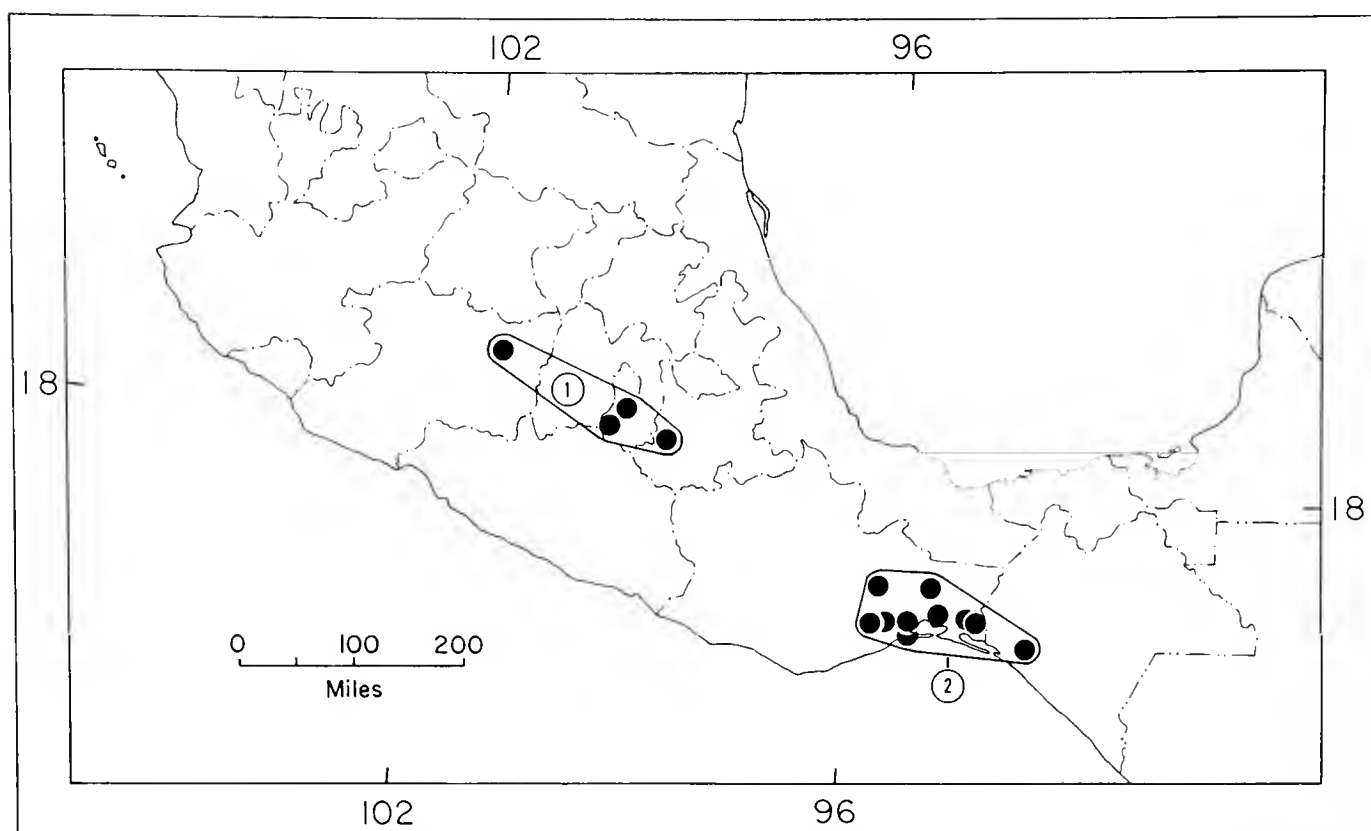


FIG. 19.—Approximate geographic areas included in the two samples of *Glossophaga morenoi* analyzed. See text for localities included in each sample.

significantly different in both sexes between the samples, and breadth of braincase also is significantly different in females between the samples.

Pelage coloration.—Individuals from Michoacán, Morelos, and Puebla (1) average darker than those from Oaxaca and Chiapas (2), in part due to less distinctly bicolored dorsal pelage. Specimens from sample 2 appear paler because the bases of the individual hairs are almost white, whereas those in specimens from sample 1 are more cream-colored.

Qualitative cranial characters (Table 5).—Pterygoid alae were absent (64.2 percent) or modestly developed (34.3 percent) in *G. morenoi*, being well developed in only one of 71 (1.5) specimens examined. Specimens from Oaxaca and Chiapas (2) have a higher incidence of moderate development of alae. The presphenoid ridge is flattened subterminally (75.0 percent) or only moderately developed (23.5 percent) in *G. morenoi*. One of 68 (1.5 percent) specimens possessed a continuous and prominent presphenoid ridge. This character exhibits little geographic variation.

The lower incisors usually are of medium size (96.8 percent) in *G. morenoi*, but they are small and paired in one (1.6 percent) and small and evenly spaced in one (1.6 percent) of 64 individuals. Little geographic variation is evident in this character.

The upper incisors are greatly procumbent (79.1 percent) or procumbent (16.4 percent); they are not noticeably procumbent in only three of 67 (4.5 percent) individuals. The angle of projection in the upper incisors tends to be less pronounced in specimens from Michoacán, Morelos, and Puebla (1). The upper incisors are un-

TABLE 15.—*Geographic variation in external and cranial measurements between two samples of Glossophaga morenoi. See text and Figure 19 for key to sample numbers.*

Measurement	Sample number	Males				Females			
		N	Mean	Range	2SD	N	Mean	Range	2SD
Length of forearm	1	5	33.92	32.5–35.8	2.44	6	34.03	32.9–35.6	2.18
	2	35	34.41	32.0–36.5	1.84	22	34.76	33.6–35.8	1.20
Length of third metacarpal	1	5	34.30	33.7–35.0	1.12	6	34.38	33.1–36.1	2.70
	2	35	34.63	32.4–36.4	2.05	22	34.87	33.0–36.1	1.45
Length of fourth metacarpal	1	5	31.86	30.8–32.9	2.00	6	31.82	30.4–35.1	3.68
	2	34	31.90	30.5–33.8	1.66	22	32.14	30.5–33.3	1.38
Length of fifth metacarpal	1	5	31.04	29.7–32.7	2.81	6	30.87	29.8–32.6	2.29
	2	35	31.11	29.4–32.7	1.88	22	31.62	30.1–32.9	1.32
Greatest length of skull	1	6	21.35	20.7–21.9	1.06	6	21.37	20.9–21.7	0.62
	2	2	21.94	21.1–22.7	0.69	22	22.06	21.3–22.6	0.64
Condylobasal length	1	6	19.77	19.2–20.2	0.85	5	19.86	19.4–20.4	0.77
	2	33	20.35	19.6–21.5	0.75	22	20.60	19.9–21.2	0.63
Zygomatic breadth	1	4	9.28	9.0–9.5	0.41	4	9.15	8.6–9.5	0.77
	2	29	9.57	9.1–10.1	0.45	16	9.47	9.0–9.7	0.37
Length of rostrum	1	6	8.65	8.4–8.8	0.33	6	8.68	8.4–9.0	0.50
	2	34	8.99	8.7–9.4	0.39	22	9.10	8.7–9.4	0.40
Mastoid breadth	1	6	8.80	8.5–9.1	0.40	5	8.70	8.1–9.1	0.85
	2	33	8.98	8.6–9.5	0.36	21	9.00	8.6–9.4	0.38
Interorbital breadth	1	6	4.07	4.0–4.3	0.24	6	4.13	4.0–4.3	0.30
	2	34	4.19	3.8–4.5	0.30	22	4.15	3.8–4.3	0.29
Breadth of braincase	1	6	8.50	8.3–8.9	0.46	5	8.42	8.1–8.8	0.52
	2	34	8.60	8.3–9.0	0.34	21	8.61	8.2–8.9	0.32
Depth of braincase	1	6	6.80	6.5–7.1	0.44	4	6.68	6.5–6.9	0.34
	2	33	6.83	6.5–7.2	0.29	21	6.83	6.4–7.2	0.36
Length of maxillary toothrow	1	6	7.40	7.2–7.6	0.31	6	7.55	7.3–7.8	0.37
	2	34	7.69	7.4–8.0	0.26	22	7.82	7.5–8.0	0.31
Length of mandibular toothrow	1	6	7.87	7.6–8.0	0.35	6	7.92	7.7–8.2	0.39
	2	35	8.15	7.8–8.5	0.29	22	8.22	7.8–8.5	0.35
Width across molars	1	6	5.63	5.6–5.7	0.10	5	5.64	5.4–5.8	0.36
	2	34	5.71	5.4–6.0	0.29	22	5.73	5.5–6.0	0.26
Mandibular length	1	6	13.85	13.7–14.0	0.28	6	14.08	13.7–14.5	0.60
	2	34	14.37	13.9–15.1	0.51	21	14.54	13.9–15.0	0.55

equal (81.6 percent) or subequal (15.4 percent) in size, the inner pair the larger, in *G. morenoi*. Two of 65 (3.0 percent) specimens have upper incisors that are equal in bulk, and these individuals are both from sample 2 (Oaxaca and Chiapas).

Basisphenoid pits are moderately deep (54.4 percent) or shallow (29.4 percent) in *G. morenoi*, but 11 of 68 (16.2 percent) individuals possess deep basisphenoid pits. Specimens from Oaxaca and Chiapas (2) have pits that average shallower relative to those from Michoacán, Morelos, and Puebla (1).

The upper premolars are unequal (58.0 percent), the second being larger than the first, or subequal (37.7 percent) in *G. morenoi*. Specimens from sample 2 (Oaxaca and Chiapas) tend to have narrower fourth upper premolars, and the three of 69 (4.3 percent) individuals with upper premolars equal in bulk are from this sample.

The slope of rostrum to braincase is gradual (75.4 percent), continuous (15.9 percent), or moderate (8.7 percent). Little geographic variation is evident in this character. Postpalatal processes are poorly developed (46.4 percent), moderately developed (24.6 percent), or greatly developed (23.2 percent) in *G. morenoi*, being absent in four of 69 (5.8 percent) individuals. This character also exhibits little geographic variation.

Taxonomic Conclusions

Patterns of geographic variation in quantitative and qualitative characters and differences in pelage coloration indicate that populations of *G. morenoi* in the mountains of Michoacán, Morelos, and Puebla are distinct from those of eastern Oaxaca and western Chiapas. Bats from the lowlands of the Isthmus of Tehuantepec, to which the trinomial *Glossophaga morenoi mexicana* Webster and Jones applies, average larger in all measurements examined, particularly those that reflect cranial length, and exhibit greater contrast in the bicolored dorsal pelage. The bases of the individual hairs are whitish and the tips are dark. In addition, these populations have shallower basisphenoid pits, narrower fourth upper premolars, and the incisors are more noticeably procumbent.

Bats from Michoacán, Morelos, and Puebla represent another subspecies, *Glossophaga morenoi morenoi* Martínez and Villa-R., that is characterized by its smaller size, shorter and narrower rostrum, deeper basisphenoid pits, better developed posterolingual cingular shelf of P4, and less distinctly bicolored dorsal pelage. The pterygoid alae tend to be absent more often and the upper incisors are not as noticeably procumbent in this subspecies as in *G. m. mexicana*.

Glossophaga morenoi mexicana Webster and Jones

1980. *Glossophaga mexicana* Webster and Jones, Occas. Papers Mus., Texas Tech Univ., 71:6, 7 November.

1986. *Glossophaga morenoi mexicana*, Gardner, Proc. Biol. Soc. Washington, 99:491, 17 October.

Holotype.—Adult female, skin and skull, MSB 27563, from Río Guamól, 34 mi. S (by Hwy. 190) La Ventosa Jct., Oaxaca, México; obtained on 27 July 1968 by M. A. Bogan, original no. 870. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Total length, 69; length of tail, 10; length of hind foot, 9.6; length of ear from notch, 13.8; length of forearm (dry), 35.2; greatest length of skull, 22.0; condylobasal length, 20.4; zygomatic breadth, 9.4; mastoid

breadth, 9.4; interorbital breadth, 4.1; length of maxillary toothrow, 7.9; length of mandibular toothrow (c-m3), 8.3.

Distribution.—This race is known from south-central and eastern Oaxaca and western Chiapas (Fig. 20); known altitudinally from sea level to approximately 1000 meters in elevation, but most records are from less than 300 meters.

Comparisons.—*Glossophaga morenoi mexicana* can be distinguished from *G. m. morenoi* by its larger size, especially measurements reflecting cranial length, and by its distinctly bicolored dorsal pelage. The bases of the individual hairs in *G. m. mexicana* are whitish and in sharp contrast with the darker tips as opposed to the cream-colored bases, which exhibit less contrast with the dark tips in *G. m. morenoi*. The basisphenoid pits average shallower and the fourth upper premolars are narrower in *G. m. mexicana* than in *G. m. morenoi*, and the upper incisors are more noticeably procumbent in *G. morenoi mexicana*.

Specimens from Puerto Angel, Oaxaca, exhibit intergradation between *morenoi* and *mexicana*; however, they are included in the latter because they have relatively long rostra, whereas those from approximately 75 kilometers to the west (0.5 mi. SE San Gabriel Mixtepec, and Puerto Escondido to San Pedro Mixtepec) are much smaller overall and their dorsal pelage is less distinctly bicolored.

Remarks.—Average external measurements (extremes in parentheses) of 13 males, followed by those of 17 females, of *G. m. mexicana* are: total length, 64.0 (57-75), 66.6 (55-74); length of tail, 7.5 (4-19), 7.7 (3-11 in 16 specimens); length of hind foot, 10.0 (8.4-13), 10.5 (8.5-12); length of ear from notch, 13.8 (10-16, 14.2 (13-15).

Specimens examined (88).—MEXICO. *Chiapas*: Finca Ocuilapa, 10 km. SE Tonalá, 1 (LSU); 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa, 17 (TTU); 15 mi. ESE Tonalá, 2 (LACM). *Oaxaca*: Diana Liesa Cave, 3 (AMNH); Guiengola (Polito), 2 (AMNH); 13 mi. ENE Juchitán (4 mi. E Jct. 185 on Rt. 190), 2 (UMMZ); Las Vacas, 3000 ft., 1 (AMNH); 34 mi. S (by Hwy. 190) La Ventosa Jct., Río Guamól, 3 (MSB); near Mazahuito, 1 (UNAM); Maxatlán, Zacatepec, 1 (AMNH); Mogoñé, 1 (AMNH); 1 mi. E Puerto Angel, 4 (TCWC); Salina Cruz (La Ventosa), 2 (AMNH); 4 mi. NE Salina Cruz (La Ventosa), 1 (AMNH); San Bartolo, 5 (AMNH); San Carlos, 1 (AMNH); San Carlos, Las Vacas, 3000 ft., 2 (AMNH); Santa María Guiengati, 1 (AMNH); Tapanatepec, 1 (AMNH); 2 mi. E Tapanatepec, 1 (KU); 4 mi. E Tapanatepec, ca. 800 ft., 2 (TCWC); 4 mi. WNW Tapanatepec, 1 (AMNH); Tehuantepec, 3 (2 AMNH, 1 USNM); 8.9 mi. E Tehuantepec, Hwy. 190, 1 (TTU); 9 mi. NW Tehuantepec, Hwy. 190, 4 (MSB); 20 mi. W Tehuantepec, 1 (UMMZ); 20 mi. NW Tehuantepec, 1 (AMNH); 60 mi. NW Tehuantepec, 3 (AMNH); Tequisistlán, 3 (AMNH); Tequisistlán, Cerro Ocotepec, 4000 ft., 3 (AMNH); near Tequisistlán, 2 (UNAM); 1 mi. N Tequisistlán, ca. 800 ft., 5 (TCWC); Unión Hidalgo, 2 (AMNH); 9.5 mi. W Zanatepec at km. post 889, El Guamól, 2 (USNM); no locality, 3 (1 AMNH, 2 FMNH).

Marginal records.—MEXICO. *Oaxaca*: Mazatlán, Zacatepec; Mogoñé. *Chiapas*: 15 km. ESE Tonalá. *Oaxaca*: 1 mi. E Puerto Angel.

Glossophaga morenoi morenoi Martínez and Villa-R.

1938. *Glossophaga morenoi* Martínez and Villa-R., An. Inst. Biol., Univ. Nac. Autónoma México, 9:347, 14 November; type material from Xiutepec (Jiutepec), Morelos, México. Type and

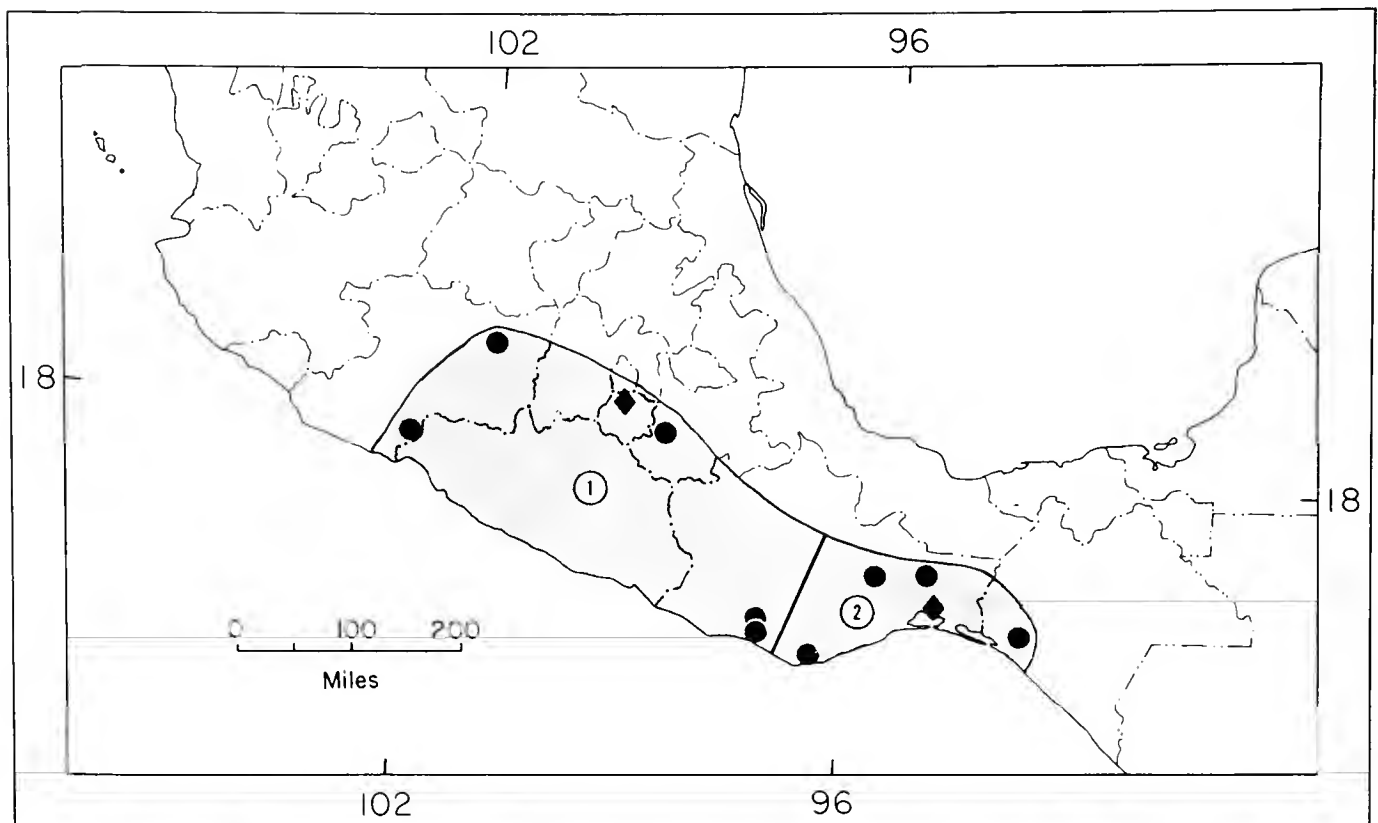


FIG. 20.—Geographic distribution of *Glossophaga morenoi morenoi* (1) and *Glossophaga morenoi mexicana* (2). Circles represent marginal localities and diamonds represent type localities.

paratypes presumably lost (Villa-R., 1953, 1964, 1967, but see Alvarez, 1966); neotype designated by Villa-R., Inst. Biol., Univ. Nac. Autónoma México, 1964:387, 25 April.

1984a. *Glossophaga mexicana brevirostris* Webster and Jones, Occas. Papers Mus., Texas Tech Univ., 91:2, 20 January; holotype from 6 mi. W Yautepec, 4500 ft., Morelos, México.

Neotype.—Adult female, skin and skull, UNAM 7383, from Cueva del Idolo, 1 km. S Tequesquitengo, 970 m., Morelos, México; obtained on 24 April 1963 by M. Villa C. (W. A. Wimsatt), original no. 37. Neotype examined; left wing of skin with perforated membranes; skull in good condition, with right auditory bulla missing.

Measurements of the neotype (Villa-R., 1964).—Total length, 69; length of tail, 6.3; length of hind foot, 10.0; length of ear from notch, 12.0; length of forearm, 34.2; condylobasal length, 20.1; breadth of braincase, 8.7.

Distribution.—This subspecies is known from Michoacán, Morelos, Puebla, Guerrero, and western Oaxaca (Fig. 20); known altitudinally from approximately 100 to 1500 meters in elevation.

Comparisons.—*Glossophaga morenoi morenoi* averages smaller than *G. morenoi mexicana* in external and cranial dimensions, particularly those of cranial length. The pelage of *G. m. morenoi*, although bicolored and similar to that found in other species of *Glossophaga*, exhibits noticeably less contrast between the pale bases and darker tips than that of *G. m. mexicana*. Furthermore, the basisphenoid pits average deeper and the fourth upper premolar has a better developed posterolingual

cingular shelf in *G. m. morenoi*, and the upper incisors are sometimes less noticeably procumbent than those found in *G. m. mexicana*.

Remarks.—The taxonomy of this species recently was reviewed by Gardner (1986), who opined that the bat named and described by Webster and Jones (1980) as *G. mexicana* was a junior synonym of *G. morenoi* Martínez and Villa-R. Central to Gardner's thesis was that Villa-R.'s designation of a neotype was consistent with Article 75 of the International Code of Zoological Nomenclature, an action considered invalid by Alvarez (1966), who thought he had rediscovered the lost type material, which he allocated to *G. soricina*. Gardner considered that the material found by Alvarez could not be associated unequivocally with the original type series; however, Gardner did not examine the specimens in question for additional clues to their provenience, and evidence (number and condition of specimens and method of preservation) presented by Alvarez (1966) agree precisely with information provided by Martínez and Villa-R. (1938). Urbano and Sánchez-H. (1983) further clouded the issue when they misidentified the neotype of *G. morenoi*, which they allocated to *G. soricina*.

I have reluctantly chosen to follow Gardner's taxonomic arrangement, but since he did not unscramble the confusion surrounding the true identity and disposition of the original type material, it deserves mention that other possible scenarios exist for this nomenclatural nightmare. Assuming the original type material is indeed lost, then the taxonomic arrangement employed herein is correct. Also, if the original type series exists and the specimens represent the species of bat described by Webster and Jones as *Glossophaga mexicana*, then the name *G. morenoi* Martínez and Villa-R. has priority. This situation is doubtful, however, because Alvarez would have noted their conspecificity with the neotype of *G. morenoi*. Assuming Alvarez correctly identified the original type material, then the name *morenoi* would be applicable to another species of bat (*G. soricina*) known from mainland Middle America; *G. soricina handleyi* Webster and Jones would become a junior synonym of *G. s. morenoi* Martínez and Villa-R., and the species of bat discussed in this chapter would be known as *G. mexicana*, with *G. m. brevirostris* Webster and Jones to the north and *G. m. mexicana* Webster and Jones to the south (see Webster and Jones, 1984a, 1985). Finally, if the original type series represents a composite of two or more species, as was the case with another glossophagine bat named by Martínez and Villa-R. (*Leptonycteris yerbabuenae*—see Ramírez-P. and Alvarez, 1972; Watkins *et al.*, 1972), then the name *Glossophaga morenoi* should be considered as a *nomen dubium* because it is impossible to determine which species of *Glossophaga* was described by Martínez and Villa-R. (1938), and three species in the genus (*G. leachii*, *G. morenoi*, and *G. soricina*) are known from Morelos. The latter possibility still exists because Alvarez (1966) extracted skulls from only two of four specimens preserved in fluid for his comparisons with the neotype of *G. morenoi*. In any event, the taxonomy of this species remains enigmatic.

Average external measurements (extremes in parentheses) of five males, followed by those of three females, of *G. m. morenoi* are: total length, 62.4 (57-67), 66.7 (65-70); length of tail, 6.6 (5-9), 7.3 (6-10); length of hind foot, 10.6 (9-12), 10.0 (9-11); length of ear from notch, 13.2 (10-16), 10.7 (10-12).

Specimens examined (24).—MEXICO. *Guerrero*: 7 km. N Balsas, 700 m., 1 (UNAM); Coyuca, 1 (UNAM); 4.5 mi. SE Cuajinicuilapa, 300 ft., 1 (MSU); 2.5 km. W Puerto Marqués, 1 (UNAM); 2 km. SW Teopan de Galeana, 120 m., 1 (UNAM); 14.5 mi. (by road) S Zumpango, ca. 2000 ft., 1 (UMMZ). *Michoacán*: 18 km. N El Infiernillo, 1 (UNAM); 12 mi. S Tzitzio, 1050 m., 1 (UMMZ). *Morelos*: Alpuyeca, 3500 ft., 1 (TCWC); Cueva del Idolo, 1 km. S Tequequitengo, 950 m., 2 (UNAM); 3 mi. N Tlayacapan, 3 (USNM); 6 mi. W Yautepec, 4500 ft., 2 (TCWC). *Oaxaca*: Puerto Escondido to San Pedro Mixtepec, 3 (AMNH); 7 mi. S Putla, 2500 ft., 1 (MSU); 0.5 mi. SE San Gabriel Mixtepec, 3 (AMNH). *Puebla*: 8 mi. SE Izucar de Matamoros, 4100 ft., 1 (MSU); 0.5 mi. SE Rífo, 1 (UMMZ).

Marginal records.—MEXICO. *Michoacán*: 18 km. N El Infiernillo; 12 mi. S Tzitzio, 1050 m. *Morelos*: 6 mi. W Yautepec, 4500 ft. *Puebla*: 8 mi. SE Izucar de Matamoros, 4100 ft. *Oaxaca*: 0.5 mi. SE San Gabriel Mixtepec; Puerto Escondido to San Pedro Mixtepec.

Glossophaga soricina Pallas' Long-tongued Bat

This bat is widely distributed from northern México (Sonora in the west and Tamaulipas in the east, but excluding much of the Mexican Plateau) southward throughout Middle America and much of South America to Paraguay and northern Argentina (Barquez, 1985); insular populations are known from the Tres Marías Islands, Jamaica, Bequia (Grenadines), Grenada, Trinidad, and Isla Margarita (Webster and Handley, 1986).

Diagnosis

Averaging in the middle of the range for the genus in external and cranial measurements in mainland North America, smaller than average in South America east of the Andes, and larger than average on the Tres Marías Islands, Jamaica, and the west coasts of Ecuador and Perú; upper incisors noticeably procumbent, I1 larger than I2 in bulk; fourth upper premolar with conspicuous posterolingual cingular shelf; parastyle of M1 well developed and directed anterolabially from paracone; mesostyle of M1 and M2 well developed; lower incisors large and usually in contact; anterior border of premaxillae elongate; pterygoid alae present; presphenoid ridge high and complete throughout; mandibular symphyseal ridge well developed; postpalatal processes usually well developed; pelage Avellaneous to Fuscous Black dorsally, Tilleul Buff to Fuscous ventrally (or Amber Brown dorsally and Army Brown ventrally in specimens with fur bleached from ammonia concentrations in roosts). Comparisons between *G. soricina* and *G. commissarisi*, *G. leachii*, *G. longirostis*, and *G. morenoi* can be found in the accounts of those species, respectively.

Ecology

Glossophaga soricina is widely distributed throughout the New World tropics and is relatively abundant in much of its range. Therefore, certain aspects of its biology have been studied extensively and are relatively well known. It would be impractical, if not impossible (see Mares and Braun, 1986), to cite the numerous accounts in the literature, many anecdotal, concerning this species. However, some past investigations are of particular importance because they dealt with multiple aspects of the biology of *G. soricina*, or they consolidated previous studies on a single topic. Major emphasis, therefore, was placed on revisionary or review manuscripts, but other records considered by me to be extremely unusual or meritorious also are included.

Glossophaga soricina occurs in a wide variety of habitats, ranging from arid subtropical thorn forests to tropical rainforests and savannas, and is distributed altitudinally from sea level to approximately 2600 meters in elevation. Xeric areas that have been colonized include the Yucatán Peninsula and the west coast of South America, as well as the relatively dry Tres Mariás Islands, Jamaica, and west coast of México. *G. soricina* also has invaded successfully the evergreen rainforests of Central America, the west coast of Colombia, and the Amazon Basin. *G. soricina* is not known to migrate, except possibly for seasonal shifts in habitat (Bonaccorso, 1979; Ramirez-Pulido and Armella, 1987), so it apparently is limited in distribution, both to the north and south, by extreme conditions in the physical environment and food habits (McNab, 1982).

Caves, tunnels, culverts, abandoned mines, hollow trees and logs, and unoccupied buildings serve as daytime roosts, and *G. soricina* also has been collected from drainage pipes and under bridges. It usually roosts in small to intermediate-sized colonies of both sexes, but females and their young reportedly form large maternity colonies during appropriate times of the year. Other species of bats such as *Artibeus jamaicensis*, *Desmodus rotundus*, *Natalus stramineus*, and most frequently *Carollia perspicillata* (Graham, 1988) share daytime roosts with *G. soricina*, but this list includes more than 30 species including *G. longirostris*. *G. soricina* also has been taken in mist nets set over water, in arroyos, and in and around forests and plantations of cultigens. In Venezuela (Handley, 1976), specimens were collected in moist (83 percent) or dry (17 percent) situations; in open habitats such as savannas, orchards, and pastures (60 percent), evergreen forests (31 percent), and deciduous forests (nine percent); and from sea level to 1560 meters in elevation, although 85 and 97 percent of the individuals taken were from less than 500 and 1000 meters, respectively.

The opportunistic dietary preferences of *G. soricina* are relatively well known (Gardner, 1977). Insects, nectar, pollen, flower parts, and fruit commonly are consumed, and fluctuations in the numbers of available insects and flowers at any given time dictate which will constitute the majority of each meal. There is ap-

parently a temporal shift in items that are consumed in Costa Rica and Panamá, in that during the dry season *G. soricina* consumes pollen, nectar, and insects, whereas fruit becomes more important during the rainy season (Fleming *et al.*, 1972; Howell and Burch, 1974; Bonaccorso, 1979). According to Alvarez and Gonzales Q. (1970), pollen is more important as food in habitats around 800 meters in elevation in México, but seldom is consumed in lowland habitats. In captivity, *G. soricina* consumed fruit equaling three times the bat's mass during a three-hour interval (Bonaccorso and Gush, 1987). The report of matted hair and flesh in the stomach of one *G. soricina* from Colombia (Arata *et al.*, 1967) may not reflect a normal dietary item but rather an act of cannibalism between the times it was caught and sacrificed (Gardner, 1977).

Glossophaga soricina exits its daytime roost shortly after sunset, and apparently is most active during the first hour of darkness and again just before sunrise in Costa Rica (LaVal, 1970) or during the second and third hours after sunset in Guerrero (Ramírez-Pulido and Armella, 1987). Individuals forage alone (Heithaus *et al.*, 1974) and actively defend foraging territories early in the evening when nectar volume is greatest, but they tend to utilize trap-line foraging behavior later in the evening after the nectar volume is depleted (Lemke, 1984; Ramírez *et al.*, 1984) or if plant resources are particularly abundant (Fleming, 1982). If plant resources are scarce, bats forage over a wider area and consume a greater variety of food items (Fleming *et al.*, 1972; Heithaus *et al.*, 1975). For example, 34 different species of plants (identified from pollen grains) were consumed by *G. soricina* in México during the months from February through July, and in September and December (Alvarez and Gonzales Q., 1970). The importance of *G. soricina* in pollination and seed dispersal has been well documented (Heithaus *et al.*, 1982; Lemke, 1985; Ramírez *et al.*, 1984; Sazima and Sazima, 1987).

The pattern of reproduction in *G. soricina* has been studied extensively (Rasweiler, 1972, 1973, 1974; Willig, 1985; Wilson, 1979). Ovulation is spontaneous and the menstrual cycle lasts 22 to 26 (mode 24) days. Menstruation, estrus, and ovulation occur approximately at the same time. Although both ovaries are functional, there is a tendency for ovulations to alternate between them. Only one ovum is released at a time, but twins have been reported in a female from Chiapas (Barlow and Tamsitt, 1968). The fertilized ovum implants in the intramural oviduct (not the uterus) in about 15 days. Length of gestation probably is two to three months, but this has not been determined accurately. Because *G. soricina* is widely distributed and patterns of reproduction over wide geographic areas can be misleading, reproductive information is presented in the account of each subspecies.

The physiological ecology of *G. soricina* also is relatively well known. Wild-caught specimens have a high basal metabolic rate and apparently are not efficient thermoregulators, as is the case in other species of nectivorous bats thus far studied. One male from Panamá did not recover from hypothermia at an ambient tempera-

ture of 6°C (Studier and Wilson, 1970). Laboratory-reared individuals, however, thermoregulated effectively at various ambient temperatures (McNab, 1969). When deprived of food for one night, captive bats become torpid and cluster with conspecifics (Rasweiler, 1973). McNab (1976) found little temporal variation in the amount of body fat in bats from Jamaica; however, Studier (1970) reported a steady decrease in body weight throughout the day due to loss of evaporative water.

Glossophaga soricina has been found to carry bacterial (*Samonella*), fungal (*Histoplasma*, *Microsporum*, *Scopulariopsis*, *Trichophyton*, and *Trichosporon*), protozoan (*Trypanosoma*), and viral (yellow fever and rabies) diseases (Jones, 1976). Endoparasites reported (Sawada and Harada, 1986; Ubelaker *et al.*, 1977) from *G. soricina* include protozoans (*Polychromophilus deanei*, *Trypanosoma cruzi*, *T. "cruzi-like," T. evansi*, *T. "rangeli-like," T. "megadermae-type,"* and *T. vespertilionis*), nematodes (*Litomosoides* sp., *L. brasiliensis*, *L. fosteri*, and *L. guiterasi*), and cestodes (*Oohoristica immatura*, *Mathevotaenia boliviana*, and *Vampirolepis elongatus*). Ectoparasites reported (Goff and Brennan, 1982; Martyn, 1988; Webb and Loomis, 1977) include macronyssid mites (*Macronyssoides kochi* and *Steatonyssus joaquimi*), a spinturnicid mite (*Periglischrus caligus*), spelaeorhynchids (*Spelaeorhynchus praecursor* and *S. hutsoni*), an ixodid tick (*Amblyomma* sp.), an argasid tick (*Ornithodoros aztecii*), a psorergatid mite (*Psorergatoides glossophagae*), trombiculid mites (*Beamerella acutascuta*, *Hooperella saccopteryx*, *H. vesperuginis*, *Loomisia desmodus*, *L. spoessi*, *L. univari*, *Microtrombicula boneti*, *Nycterinastes primus*, *Perissopalla beltrani*, *P. exhumatus*, *P. precarria*, *P. rationalis*, *Speleocola davisii*, *S. secunda*, *Wagenaaria similis*, and *Whartonia nudosetosa*), a labidocarpid mite (*Alabidocarpus furmani*), a sarcoptid mite (*Chirnyssoides caparti*), and streblid batflies (*Paradyschiria parvuloides*, *Speiseriae ambigua*, *Strebla carolliae*, *S. mirabilis*, *Trichobius dugesii*, *T. furmani*, *T. joblingi*, *T. longipes*, and *T. uniformis*).

Other aspects of the biology of *G. soricina* that have been examined include the morphology of the brain (McDaniel, 1976), cochlea (Pye, 1967, 1980), hyoid and lingual musculature (Griffiths, 1982; Wille, 1954), salivary glands (Phillips *et al.*, 1987), alimentary tract (Forman, 1972; Forman *et al.*, 1979; Mennone *et al.*, 1986; Zharova, 1990), sperm (Forman, 1968; Forman and Genoways, 1979), female reproductive system (Hood and Smith, 1982), wing (Smith and Starret, 1979), and nucleolar organizing region (Moriella and Varella-Garcia, 1988), as well as dental (Phillips, 1971) and oral biology (Phillips *et al.*, 1977), the composition of the milk (Jenness and Studier, 1976), and retinal neurotransmitters (Studholme *et al.*, 1987). *Glossophaga soricina* has been used extensively in echolocation research (Griffin, 1958; Griffin and Novick, 1955; Howell, 1974; Novick, 1963) and the investigation of circadian activity rhythms (Erkert, 1982; Erkert *et al.*, 1980).

Geographic Variation

Univariate Analyses

Adult specimens from throughout the geographic range of *G. soricina* were grouped into 32 samples (see Figs. 21-22) as follows: *sample 1*—NAYARIT (Tres Mariás Islands); *sample 2*—SONORA, SINALOA, CHIHUAHUA, and DURANGO; *sample 3*—NAYARIT (mainland), ZACATECAS, JALISCO, and COLIMA; *sample 4*—TAMAULIPAS, SAN LUIS POTOSI, QUERETARO, and HIDALGO; *sample 5*—MEXICO, DISTRITO FEDERAL, MORELOS, and GUERRERO; *sample 6*—VERACRUZ and PUEBLA; *sample 7*—OAXACA; *sample 8*—TABASCO and CHIAPAS; *sample 9*—CAMPECHE, YUCATAN, QUINTANA ROO, and BELIZE; *sample 10*—GUATAMALA and EL SALVADOR; *sample 11*—HONDURAS; *sample 12*—NICARAGUA; *sample 13*—COSTA RICA and PANAMA (Bocas del Toro and Los Santos); *sample 14*—PANAMA (Darién) and COLOMBIA (Antioquia, Bolívar, and Magdalena); *sample 15*—COLOMBIA (Valle del Cauca and Nariño); *sample 16*—ECUADOR (Manabí, Guayas, Loja, Los Ríos, and El Oro); *sample 17*—PERU (Piura, Lambayeque, and Cajamarca); *sample 18*—PERU (Ancash, Lima, and Arequipa); *sample 19*—PERU (upper Marañón River Valley in Amazonas); *sample 20*—COLOMBIA (Magdalena River Valley in Tolima and Huila); *sample 21*—VENEZUELA; *sample 22*—GUYANA, SURINAME, and FRENCH GUIANA; *sample 23*—ECUADOR (Napo) and PERU (Loreto, Amazonas, and San Martín); *sample 24*—PERU (Pasco and Cuzco); *sample 25*—BRAZIL (Amazonas); *sample 26*—BRAZIL (Pará and Maranhão); *sample 27*—BRAZIL (Mato Grosso and Goiás); *sample 28*—BRAZIL (Rio Grande do Norte, Minas Gerais, and São Paulo); *sample 29*—BOLIVIA; *sample 30*—PARAGUAY; *sample 31*—JAMAICA; *sample 32*—TRINIDAD. Standard statistics for all geographic samples are given in Table 16, and the results of four (length of forearm, greatest length of skull, width across molars, and mandibular length) SS-STP tests are given in Table 17.

External measurements.—Specimens from western Perú (samples 17-19), Jamaica (31), and the Tres Mariás Islands (1) average much larger than those from other populations in measurements of the wing (Table 16). Bats from mainland North America and northern Colombia (2-14), western Ecuador (16), Trinidad (32), Bolivia (29), and Paraguay (30) average in the middle of the range for the species, but there is clinal variation in external dimensions in that specimens from northern México are larger than those from Central America. Specimens from the remainder of South America (15, 20-28) are smaller than average.

Cranial measurements.—Greatest length of skull, condylobasal length, length of rostrum, length of maxillary toothrow, length of mandibular toothrow, and mandibular length exhibit similar patterns of geographic variation (Table 16). Specimens from western Ecuador and Perú (16-19), Jamaica (31), and the Tres Mariás Islands (1) are larger than average for the species in these dimensions,

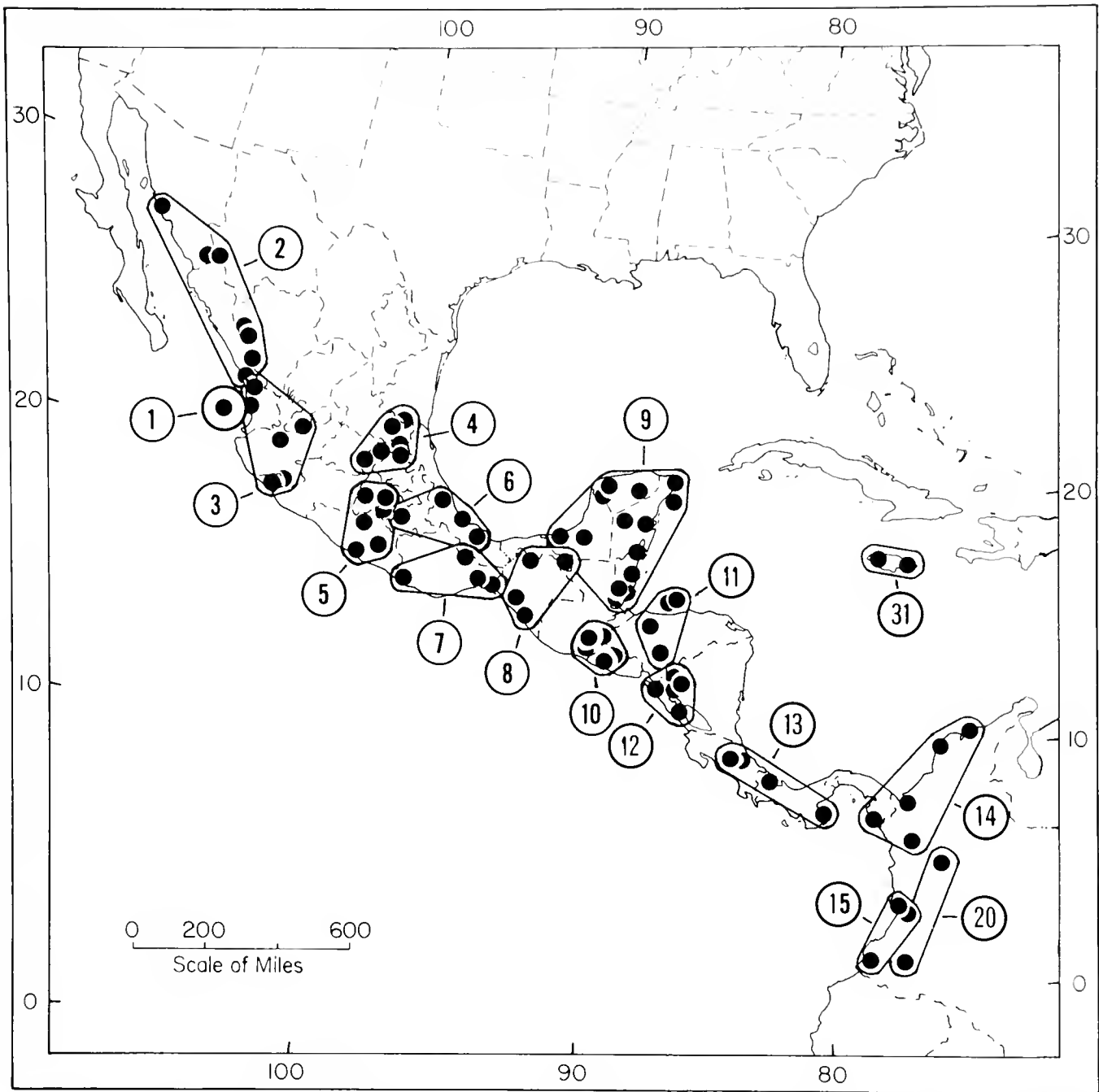


FIG. 21.—Approximate geographic areas in North America included in some of the 32 samples of *Glossophaga soricina* analyzed. See text for localities included in each sample.

whereas those from South America east of the Andes (21-30), Trinidad (32), and the Magdalena River Valley (20) are smaller than average. Specimens from the North American mainland (2-13) and northern and western Colombia (14-15) are intermediate in measurements of cranial length.

Specimens from Jamaica (31), particularly males, the west coasts of Ecuador and Perú (16-19), and females from western Colombia (15) are larger than average for the species in most measurements of cranial width (zygomatic breadth, interorbital breadth, and width across molars). Specimens from the Magdalena River Valley (20), South America east of the Andes (21-30), and Trinidad (32) tend to be smaller than average in these dimensions, whereas those from the remaining samples (1-15) average in the middle of the range for the species.

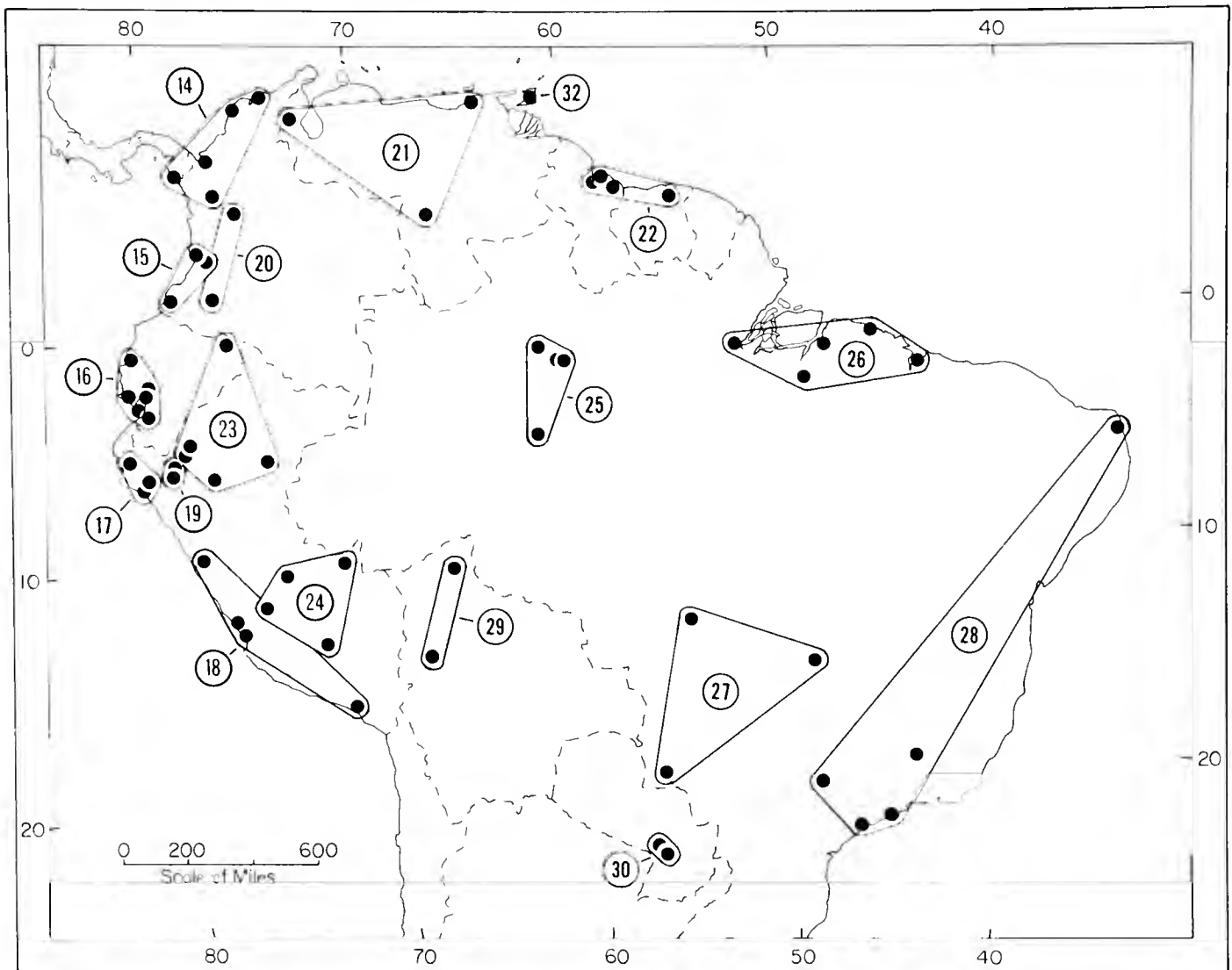


FIG. 22.—Approximate geographic areas in South America included in some of the 32 samples of *Glossophaga soricina* analyzed. See text for localities included in each sample.

The pattern of geographic variation in mastoid breadth is similar to that mentioned in the preceding paragraph except that specimens from Jamaica (31) and the upper Marañón River Valley (19) average in the middle of the range for the species.

Breadth of braincase exhibits no discernible pattern of geographic variation. Specimens from Jamaica (31), western Ecuador (16), southwestern Perú (18), and females from eastern Brazil (28), and Guatamala and El Salvador (10) are, in general, larger than average for the species. Those from the Magdalena River Valley (20), Venezuela (21), Trinidad (32), the Guianas (22), Amazonian Ecuador and Perú (23), and western Brazil (25) are smaller than average. Specimens from other samples in North and South America tend to average in the middle of the range for the species in breadth of braincase.

Depth of braincase also exhibits no particular pattern in geographic variation. Specimens from northern Colombia (14); southwestern Perú (18), females from Guatamala and El Salvador (10), and males from Puebla and Veracruz (6) are much larger than average for the species. Individuals from samples 32 (Trinidad), and 23 and 24 (Amazonian Ecuador and Perú) tend to be smaller than average in braincase depth. Specimens from all other samples are intermediate in size.

TABLE 16.—*Geographic variation in external and cranial measurements among 32 samples of Glossophaga soricina. See text and Figures 21–22 for key to sample numbers.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of forearm</i>								
1	16	36.42	35.2–37.8	1.18	14	37.26	36.4–38.2	1.05
2	9	35.31	33.8–36.8	1.89	21	36.39	35.0–37.7	1.59
3	39	35.33	33.6–36.4	1.50	45	36.00	34.3–37.6	1.70
4	14	35.85	34.4–37.4	1.76	25	36.16	34.3–37.5	1.60
5	9	35.71	34.0–37.2	2.22	15	36.23	34.4–38.2	2.13
6	10	35.65	34.5–37.2	1.70	9	35.29	34.6–36.2	1.02
7	12	34.78	33.4–36.3	1.40	21	35.67	34.2–36.7	1.30
8	12	35.58	33.7–37.1	1.88	13	35.60	34.1–37.4	1.79
9	36	34.89	33.2–36.2	1.28	20	35.39	33.3–37.2	1.81
10	15	35.01	33.7–36.2	1.54	11	35.79	34.9–36.5	1.15
11	10	34.80	33.1–36.1	2.29	10	35.38	33.9–36.5	1.81
12	13	35.46	33.4–37.7	2.19	14	35.70	34.1–37.1	1.59
13	26	35.11	33.9–36.7	1.77	15	35.51	33.8–37.0	2.08
14	10	34.77	33.8–35.5	1.29	6	35.30	34.2–35.9	1.25
15	6	34.57	34.0–36.3	1.76	6	34.87	33.2–36.1	2.01
16	30	34.96	31.8–37.5	2.44	20	36.29	34.6–37.8	1.97
17	6	36.13	35.0–37.5	2.08	8	37.04	36.3–37.9	1.05
18	5	36.74	35.1–38.2	2.28	9	37.96	35.5–39.4	1.77
19	7	36.60	36.0–37.8	1.31	9	37.48	36.0–39.8	2.50
20	6	33.93	33.2–35.5	1.75	4	35.93	35.1–36.5	1.18
21	6	34.23	32.8–35.2	1.92	9	33.80	32.2–35.4	2.31
22	14	34.71	34.2–35.8	0.84	17	34.15	32.8–36.0	1.71
23	19	34.41	33.1–35.8	1.52	10	34.35	33.7–35.2	0.93
24	5	34.22	32.9–35.1	1.81	4	35.10	33.5–36.3	2.47
25	20	34.08	32.3–36.2	1.61	21	35.09	33.4–36.9	1.89
26	4	34.98	34.1–35.8	1.54				
27	10	33.50	32.2–34.5	1.35	5	34.82	33.3–36.5	2.57
28	5	34.32	33.3–36.1	2.36	7	34.63	31.7–36.9	3.36
29	6	34.98	33.8–35.9	1.63	8	35.71	34.8–36.6	1.23
30	13	34.73	34.1–35.7	1.03	15	34.93	34.2–36.3	1.43
31	8	36.51	35.9–37.4	0.99	10	37.18	36.3–38.4	1.24
32	9	34.69	33.6–36.0	1.79	8	36.26	33.0–38.0	2.99
<i>Length of third metacarpal</i>								
1	16	36.03	34.2–37.4	1.76	14	36.69	35.4–37.8	1.41
2	9	35.69	34.0–37.6	2.41	21	36.76	34.0–38.7	2.29
3	39	35.34	32.8–37.1	1.90	45	36.15	33.8–37.9	1.81
4	14	35.89	31.5–34.7	1.65	25	35.65	34.7–36.6	1.12
5	9	36.43	35.4–37.8	1.64	15	36.03	34.3–37.7	2.01
6	10	35.94	35.6–36.6	0.62	9	35.34	33.9–36.2	1.30
7	12	35.40	32.9–36.8	2.29	21	36.04	34.7–37.0	1.36
8	12	35.68	34.1–37.3	1.90	13	35.88	32.9–37.1	2.11
9	36	34.99	33.5–37.1	1.62	20	35.43	32.1–36.6	2.17

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
10	15	35.05	33.6–36.9	1.90	11	35.74	34.5–36.8	1.68
11	10	35.19	32.5–37.0	2.39	10	35.76	34.6–37.7	1.87
12	13	35.63	34.8–36.3	1.02	14	35.89	33.4–37.1	1.92
13	26	35.57	33.7–37.9	2.17	15	35.71	34.3–37.3	1.90
14	10	34.97	33.2–36.3	2.07	6	35.55	35.0–36.3	1.05
15	6	35.17	34.0–36.8	1.95	6	34.80	33.2–36.4	2.09
16	30	35.57	33.6–37.1	1.72	20	36.32	33.6–39.1	2.57
17	6	36.47	35.3–37.5	1.70	8	37.28	36.2–39.3	1.96
18	5	37.22	36.2–38.5	2.17	9	38.02	36.3–39.5	1.83
19	7	36.77	36.1–37.6	1.10	9	37.49	36.0–39.4	2.38
20	6	34.43	33.6–35.5	1.69	4	36.25	36.0–36.7	0.62
21	6	34.08	32.4–35.4	2.55	9	33.83	32.5–35.4	2.05
22	15	34.97	34.2–35.8	1.87	17	34.76	33.7–36.0	1.50
23	19	34.72	33.0–36.4	1.99	10	34.32	33.4–35.5	1.39
24	5	34.36	33.8–35.0	0.92	4	34.83	33.2–37.0	3.40
25	20	34.25	32.2–36.2	1.61	22	35.09	33.4–36.6	1.59
26	5	34.34	33.5–35.9	1.93				
27	10	33.61	32.2–34.7	1.88	5	34.96	33.5–36.5	2.61
28	5	34.82	34.0–35.7	1.44	7	35.20	32.9–37.1	2.92
29	6	34.78	32.9–35.6	2.35	8	35.46	34.4–36.4	1.46
30	13	34.98	32.6–36.1	1.98	15	35.69	34.5–36.9	1.53
31	8	36.94	36.1–38.1	1.13	10	37.44	35.9–38.7	1.51
32	9	34.52	32.4–36.3	2.40	8	36.46	33.5–38.1	2.72
<i>Length of fourth metacarpal</i>								
1	16	33.01	32.2–34.6	1.48	14	33.86	32.9–34.9	1.32
2	9	32.34	30.9–34.2	2.40	21	33.80	32.2–35.6	2.13
3	39	32.44	30.4–34.0	2.01	45	33.23	31.5–34.9	1.63
4	14	32.95	31.5–34.7	1.91	25	32.73	31.4–34.1	1.24
5	9	33.14	32.1–34.6	1.61	15	33.04	31.4–34.3	1.64
6	10	32.88	31.8–34.0	1.35	9	32.54	31.2–33.3	1.32
7	12	32.43	30.0–34.2	2.34	21	32.93	30.8–34.2	1.55
8	12	32.70	31.1–34.3	1.80	13	32.72	31.3–34.2	1.54
9	36	32.01	30.2–33.8	1.53	20	32.44	30.8–33.8	1.45
10	15	32.29	30.8–33.7	1.46	11	32.96	31.7–34.7	1.79
11	10	32.24	31.2–33.1	1.25	10	32.98	31.9–34.8	1.98
12	13	32.60	31.4–33.8	1.62	14	32.89	30.9–34.5	1.91
13	26	32.65	30.3–34.9	2.28	15	32.94	31.5–34.8	2.08
14	10	32.35	31.0–33.5	1.72	6	32.62	31.8–33.4	1.09
15	6	32.05	31.4–33.5	1.61	6	31.70	31.3–32.2	0.70
16	30	32.60	31.1–34.4	1.68	20	33.58	31.4–35.6	2.26
17	6	33.42	31.9–34.8	1.87	8	34.64	33.8–35.6	1.38
18	5	34.26	32.7–35.7	2.70	9	35.29	33.4–36.3	1.60
19	7	34.00	33.3–35.6	1.51	9	34.52	33.2–36.5	2.13
20	6	31.27	30.6–31.9	1.16	4	33.15	32.6–33.4	0.74

TABLE 16.—*Continued.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
21	6	31.40	29.7–32.9	2.69	9	31.17	30.0–32.2	1.83
22	15	31.91	29.2–33.4	2.35	17	31.72	30.6–32.8	1.40
23	19	31.79	29.9–32.6	1.63	10	31.47	30.2–33.1	1.71
24	5	31.46	30.9–32.2	1.06	4	31.88	30.4–33.4	2.61
25	20	31.38	29.9–32.9	1.36	22	32.21	30.7–33.5	1.67
26	5	31.68	29.9–34.5	3.43				
27	10	31.04	29.9–32.6	1.66	5	32.42	31.1–33.7	2.09
28	5	32.30	31.1–33.3	1.93	7	32.39	30.2–34.6	2.82
29	6	31.48	30.0–32.4	1.87	8	32.31	30.9–34.1	2.00
30	13	32.58	31.1–34.0	1.68	15	33.09	32.4–34.3	0.98
31	8	34.46	33.7–35.3	1.01	10	34.87	34.0–35.8	1.14
32	9	31.87	30.3–33.7	2.28	8	34.05	30.7–36.1	3.13
<i>Length of fifth metacarpal</i>								
1	16	32.09	30.4–33.5	1.72	14	32.87	31.4–34.4	1.53
2	9	31.29	29.9–33.2	2.19	21	32.49	30.8–34.1	1.83
3	39	31.25	29.3–32.7	1.67	45	32.07	29.0–33.8	1.83
4	14	31.89	30.4–34.2	2.16	25	31.70	30.8–32.8	1.21
5	9	31.96	30.7–34.4	2.21	15	32.27	31.2–34.0	1.66
6	10	31.89	31.1–32.8	1.01	9	31.42	29.2–32.3	1.89
7	12	31.18	29.5–32.9	2.02	21	31.83	30.1–33.7	1.74
8	12	31.43	29.0–32.8	2.07	13	31.79	30.2–33.7	1.83
9	37	30.99	29.1–33.0	1.55	20	31.37	29.7–32.8	1.78
10	15	31.11	30.2–32.5	1.31	11	31.79	31.1–33.0	1.32
11	10	31.06	29.9–32.4	1.73	10	31.99	31.2–33.7	1.56
12	13	31.55	30.2–32.8	1.48	14	31.85	29.7–33.8	1.89
13	26	31.48	29.8–33.5	1.81	15	31.83	30.0–33.4	2.05
14	10	31.08	29.4–31.8	1.56	6	31.82	31.3–32.3	1.04
15	6	31.10	30.3–32.6	1.78	6	30.80	29.8–31.2	0.79
16	30	31.37	29.7–33.2	1.60	20	32.64	30.9–34.9	2.19
17	6	32.63	31.3–33.8	2.02	8	33.84	33.1–35.2	1.47
18	5	33.66	32.7–34.5	1.71	9	34.26	32.4–35.7	2.11
19	7	33.10	32.3–34.6	1.54	9	33.36	31.7–35.5	2.52
20	6	30.68	30.1–31.4	1.10	4	32.28	31.8–32.6	0.72
21	6	30.53	29.2–32.0	2.45	9	30.48	29.2–31.6	1.86
22	13	31.13	30.2–32.6	1.67	17	30.75	29.6–32.0	1.53
23	19	30.95	29.1–32.2	1.63	10	30.63	29.2–32.1	1.79
24	5	30.52	29.9–31.2	1.01	4	31.18	29.8–33.0	3.08
25	20	30.44	28.9–32.2	1.33	22	31.35	29.6–33.0	2.12
26	5	30.48	28.9–32.9	2.97				
27	10	29.96	28.8–31.0	1.48	5	31.32	29.3–33.5	3.16
28	5	31.04	29.9–31.6	1.38	7	31.69	29.3–33.9	3.05
29	6	30.70	29.2–31.4	1.58	8	31.81	31.0–33.2	1.43
30	13	31.61	30.0–33.0	1.52	15	32.35	31.1–33.6	1.31
31	8	33.04	32.4–34.2	1.09	10	33.47	32.8–34.9	1.28
32	9	30.44	28.7–32.4	2.22	8	32.86	29.6–34.3	2.95

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Greatest length of skull</i>								
1	18	21.96	21.4–22.5	0.69	15	22.01	21.6–22.6	0.54
2	9	21.19	20.7–22.2	0.93	20	21.49	20.6–22.1	0.82
3	40	21.27	20.3–21.9	0.69	49	21.44	20.5–22.6	0.84
4	10	21.42	20.9–22.0	0.75	22	21.32	20.7–22.0	0.73
5	8	21.40	21.2–21.8	0.44	15	21.45	21.1–21.9	0.55
6	10	21.55	21.1–22.0	0.60	9	21.03	20.4–21.6	0.76
7	10	21.05	20.4–21.7	0.90	19	21.22	20.5–21.7	0.70
8	11	21.39	21.1–21.9	0.53	12	21.42	20.8–22.3	0.79
9	35	21.15	20.0–21.9	0.78	19	21.25	20.4–22.1	0.77
10	14	21.35	20.8–22.0	0.54	10	21.55	20.9–22.3	0.94
11	10	21.43	20.9–21.9	0.58	9	21.26	20.8–21.6	0.51
12	12	21.46	20.8–21.9	0.68	12	21.45	20.9–21.9	0.64
13	26	21.42	20.8–22.3	0.77	14	21.34	20.8–21.8	0.70
14	10	21.15	20.4–21.5	0.67	6	21.25	20.9–21.5	0.43
15	6	21.23	20.8–22.1	0.92	3	21.73	21.4–22.4	1.15
16	28	22.15	21.6–23.0	0.65	31	22.21	20.9–23.2	0.94
17	5	22.32	21.9–22.7	0.78	7	22.11	21.7–22.8	0.85
18	5	22.60	22.4–22.8	0.32	8	22.84	22.4–23.2	0.59
19	7	21.94	21.5–22.3	0.61	9	21.94	21.4–22.7	0.92
20	6	20.30	19.9–20.7	0.70	4	20.75	20.2–21.1	0.81
21	6	20.60	20.1–21.3	0.86	9	20.29	19.2–21.1	1.14
22	15	20.35	19.8–21.0	0.73	17	20.25	19.7–20.9	0.64
23	18	20.49	20.1–20.9	0.59	10	20.38	19.9–20.8	0.65
24	3	20.50	20.3–20.6	0.35	3	20.70	20.4–21.1	0.72
25	19	20.19	19.3–20.7	0.72	19	20.26	19.5–21.3	0.87
26	4	19.98	19.7–20.2	0.53				
27	9	20.06	19.0–21.1	1.12	5	20.44	20.0–21.1	0.91
28	5	20.80	20.2–21.6	1.14	6	20.77	20.3–21.4	0.72
29	6	20.23	19.7–20.5	0.62	8	20.56	20.1–21.1	0.79
30	13	20.51	19.5–20.9	0.76	11	20.76	20.3–21.2	0.57
31	7	22.21	21.5–22.8	0.82	8	22.15	20.6–22.6	1.32
32	10	20.48	19.9–21.2	0.85	9	20.89	20.1–21.7	1.06
<i>Condylbasal length</i>								
1	18	20.23	19.6–20.8	0.65	15	20.35	19.8–21.2	0.64
2	9	19.60	19.1–20.5	1.00	21	19.95	19.2–20.4	0.73
3	41	19.65	18.8–20.7	0.80	48	19.90	18.9–21.9	0.95
4	13	19.56	18.6–20.2	0.87	21	19.69	19.1–20.2	0.74
5	9	19.60	19.2–20.1	0.62	15	19.89	19.5–20.3	0.40
6	8	19.90	19.5–20.6	0.81	6	19.48	18.7–20.1	1.05
7	8	19.49	19.0–19.9	0.74	20	19.68	18.8–20.2	0.43
8	11	19.70	19.1–20.0	0.65	11	19.72	19.2–20.4	0.57
9	35	19.45	18.5–20.2	0.78	19	19.53	18.9–20.5	0.65
10	14	19.62	19.3–20.1	0.53	10	19.83	18.9–20.6	0.96

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
11	10	19.65	19.4–20.3	0.51	8	19.73	19.0–20.1	0.69
12	12	19.73	19.2–20.1	0.63	11	19.69	19.4–20.0	0.37
13	23	19.69	19.0–20.6	0.75	14	19.75	19.3–20.1	0.52
14	10	19.50	18.8–20.0	0.71	6	19.48	19.0–20.0	0.71
15	6	19.52	19.2–20.1	0.71	3	20.03	19.7–20.6	0.99
16	29	20.54	20.0–21.4	0.67	32	20.68	19.5–21.5	0.88
17	5	20.66	20.4–20.9	0.46	7	20.59	20.1–21.2	0.83
18	5	21.10	20.8–21.3	0.40	8	21.28	20.7–21.8	0.72
19	7	20.33	20.0–20.8	0.54	9	20.47	19.8–21.3	1.08
20	6	18.67	18.2–19.1	0.73	4	19.15	18.6–19.5	0.77
21	6	18.92	18.6–19.8	0.89	8	18.76	17.8–19.6	1.31
22	15	18.65	18.1–19.0	0.58	17	18.68	18.2–19.6	0.82
23	19	18.82	18.4–19.4	0.56	10	18.82	18.4–19.2	0.62
24	4	18.93	18.8–19.1	0.25	3	19.20	19.0–19.6	0.69
25	18	18.59	17.7–19.0	0.70	19	18.66	17.6–19.5	0.89
26	5	18.52	18.2–18.8	0.46				
27	9	18.47	17.6–19.3	0.34	5	18.98	18.6–19.5	0.74
28	5	19.02	18.6–19.6	0.84	6	19.03	18.6–19.6	0.65
29	6	18.65	18.2–19.0	0.56	8	18.98	18.4–19.5	0.75
30	12	18.90	18.2–19.4	0.80	12	19.20	18.7–19.5	0.43
31	7	20.57	20.1–21.0	0.69	9	20.62	20.1–21.0	0.51
32	10	18.87	18.1–19.5	0.90	9	19.24	18.5–20.1	1.02
Zygomatic breadth								
1	16	9.45	9.0–9.8	0.48	13	9.18	8.9–9.5	0.40
2	9	9.29	8.8–9.8	0.58	20	9.40	8.9–9.8	0.55
3	40	9.33	8.7–10.0	0.57	42	9.35	8.6–9.8	0.52
4	11	9.25	8.8–9.6	0.46	17	9.35	9.0–9.8	0.45
5	8	9.39	9.1–9.7	0.46	15	9.36	9.1–9.6	0.33
6	6	9.43	9.2–9.6	0.33	4	8.98	8.7–9.3	0.64
7	10	9.17	8.7–9.8	0.57	14	9.29	8.9–9.7	0.43
8	11	9.54	9.2–9.8	0.36	11	9.24	8.7–9.7	0.57
9	33	9.38	8.8–9.9	0.46	18	9.22	8.8–9.6	0.51
10	14	9.39	9.0–9.7	0.43	10	9.43	9.1–9.7	0.41
11	9	9.47	9.1–9.9	0.57	6	9.57	9.3–9.9	0.50
12	12	9.43	9.1–9.8	0.50	10	9.31	9.1–9.7	0.48
13	25	9.40	8.7–9.9	0.57	12	9.58	9.2–9.9	0.42
14	9	9.44	9.1–9.7	0.36	5	9.38	9.2–9.7	0.43
15	4	9.58	9.4–9.7	0.25	3	9.43	9.4–9.5	0.12
16	31	9.57	9.3–9.9	0.36	30	9.51	9.0–9.8	0.45
17	5	9.72	9.6–9.9	0.26	8	9.51	9.3–9.8	0.31
18	5	9.70	9.6–9.9	0.28	8	9.75	9.5–10.3	0.48
19	7	9.43	9.2–9.6	0.32	9	9.46	9.3–9.7	0.30
20	6	8.95	8.7–9.3	0.43	4	8.90	8.7–9.1	0.37
21	6	9.22	9.0–9.4	0.34	8	8.95	8.4–9.3	0.60

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
22	15	8.87	8.5–9.3	0.47	16	8.84	8.6–9.5	0.48
23	19	8.99	8.8–9.5	0.36	10	8.96	8.7–9.2	0.32
24	5	9.02	8.8–9.2	0.36	2	9.10	9.1	0.00
25	16	8.94	8.2–9.3	0.53	18	8.96	8.7–9.4	0.39
26	5	9.04	8.8–9.3	0.36				
27	10	8.98	8.8–9.4	0.34	3	8.93	8.8–9.0	0.23
28	4	9.05	8.9–9.4	0.48	6	9.27	8.9–9.5	0.55
29	6	9.05	8.8–9.3	0.37	8	9.09	8.8–9.3	0.33
30	12	9.11	8.5–9.5	0.56	12	9.19	8.9–9.6	0.46
31	6	9.73	9.5–9.9	0.30	8	9.55	9.4–9.8	0.34
32	11	9.07	8.6–9.5	0.61	9	9.08	8.7–9.9	0.78
<i>Length of rostrum</i>								
1	18	8.82	8.5–9.1	0.40	15	8.88	8.6–9.2	0.33
2	9	8.41	8.1–9.1	0.60	22	8.67	8.3–9.0	0.36
3	41	8.47	8.1–8.9	0.40	49	8.59	8.0–9.1	0.42
4	14	8.36	7.7–8.7	0.56	23	8.57	8.2–9.0	0.46
5	9	8.48	7.9–8.7	0.51	15	8.58	8.2–8.7	0.26
6	10	8.56	8.4–8.8	0.27	8	8.44	8.2–8.6	0.24
7	11	8.38	8.1–8.9	0.45	22	8.49	8.2–8.8	0.36
8	12	8.53	8.2–8.9	0.45	13	8.58	8.2–8.8	0.35
9	37	8.41	7.8–8.8	0.42	20	8.51	8.0–8.9	0.38
10	15	8.49	8.2–8.8	0.32	10	8.63	8.1–9.1	0.52
11	10	8.43	8.2–8.7	0.30	9	8.40	8.0–8.7	0.44
12	13	8.51	8.2–8.7	0.37	14	8.60	8.2–8.9	0.39
13	26	8.47	8.2–8.9	0.35	15	8.46	8.1–8.8	0.38
14	10	8.36	7.9–8.7	0.41	6	8.33	8.0–8.5	0.37
15	6	8.43	8.2–8.7	0.41	5	8.56	8.3–9.1	0.66
16	33	8.89	8.4–9.3	0.41	32	9.02	8.6–9.5	0.48
17	5	8.98	8.6–9.2	0.46	7	8.93	8.6–9.1	0.40
18	5	9.28	9.0–9.4	0.33	8	9.36	9.0–9.7	0.44
19	7	8.87	8.6–9.2	0.43	9	8.91	8.4–9.3	0.57
20	6	8.12	8.0–8.3	0.23	4	8.20	8.0–8.5	0.43
21	6	8.12	7.9–8.5	0.43	9	8.07	7.5–8.5	0.62
22	16	7.96	7.7–8.4	0.42	17	7.97	7.6–8.5	0.52
23	19	8.07	7.8–8.4	0.38	10	8.06	7.8–8.3	0.37
24	4	8.03	7.9–8.2	0.25	4	8.40	7.1–8.7	0.52
25	20	7.93	7.4–8.3	0.41	21	8.05	7.7–8.4	0.44
26	6	7.90	7.7–8.1	0.33				
27	9	7.84	7.5–8.2	0.43	5	8.22	8.1–8.4	0.26
28	5	8.04	7.6–8.4	0.66	6	8.22	8.0–8.4	0.32
29	6	8.00	7.8–8.3	0.36	8	8.25	8.0–8.5	0.32
30	13	8.12	7.5–8.5	0.54	13	8.25	7.9–8.4	0.30
31	7	8.87	8.7–9.1	0.25	9	8.89	8.6–9.1	0.34
32	10	8.02	7.7–8.4	0.53	11	8.35	7.9–8.8	0.55

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Mastoid breadth</i>								
1	17	9.11	8.9–9.5	0.34	14	8.99	8.8–9.1	0.18
2	9	9.06	8.8–9.2	0.28	21	8.98	8.5–9.3	0.43
3	43	8.96	8.5–9.4	0.38	48	9.03	8.5–9.3	0.39
4	13	9.02	8.7–9.2	0.28	22	8.96	8.6–9.3	0.34
5	9	9.01	8.7–9.3	0.41	15	8.99	8.7–9.3	0.32
6	9	9.09	8.8–9.3	0.31	6	8.80	8.7–8.9	0.18
7	11	8.86	8.5–9.4	0.45	19	8.91	8.6–9.1	0.28
8	11	9.05	8.9–9.3	0.27	11	8.95	8.7–9.3	0.31
9	35	8.96	8.5–9.3	0.42	19	8.85	8.4–9.2	0.44
10	14	9.04	8.8–9.4	0.30	11	9.05	8.7–9.3	0.40
11	10	9.15	8.8–9.4	0.40	9	9.10	8.7–9.4	0.45
12	12	9.06	8.7–9.5	0.41	11	8.96	8.7–9.3	0.39
13	25	9.05	8.7–9.3	0.34	14	9.14	8.9–9.7	0.45
14	10	8.90	8.6–9.0	0.30	6	8.98	8.8–9.2	0.34
15	6	9.15	8.9–9.3	0.25	4	9.10	9.0–9.2	0.16
16	29	9.18	8.9–9.6	0.33	30	9.14	8.6–9.6	0.47
17	6	9.20	9.0–9.5	0.42	7	9.19	9.0–9.5	0.37
18	5	9.36	9.2–9.6	0.30	8	9.38	9.1–9.5	0.26
19	7	9.03	8.8–9.3	0.40	9	9.04	8.7–9.5	0.51
20	6	8.72	8.5–9.0	0.39	4	8.83	8.7–9.0	0.25
21	6	8.80	8.6–9.0	0.31	8	8.61	8.1–9.0	0.64
22	15	8.59	8.3–8.8	0.31	18	8.64	8.4–9.0	0.36
23	19	8.62	8.4–8.9	0.26	10	8.62	8.4–8.8	0.30
24	5	8.66	8.6–8.8	0.18	3	8.73	8.6–8.8	0.23
25	18	8.72	8.4–9.0	0.33	19	8.72	8.5–9.1	0.33
26	6	8.85	8.5–9.3	0.55				
27	10	8.73	8.4–9.1	0.38	5	8.86	8.7–9.2	0.41
28	5	8.84	8.7–9.0	0.23	6	8.80	8.7–9.0	0.25
29	6	8.68	8.4–8.9	0.43	8	8.73	8.5–8.9	0.35
30	12	8.80	8.6–9.1	0.31	13	8.92	8.6–9.3	0.38
31	7	8.99	8.6–9.2	0.41	10	9.02	8.8–9.3	0.28
32	11	8.65	8.4–9.0	0.39	10	8.72	8.4–9.2	0.55
<i>Interorbital breadth</i>								
1	18	4.14	3.8–4.5	0.32	15	4.12	3.9–4.3	0.20
2	9	4.12	3.9–4.3	0.26	22	4.17	3.9–4.5	0.31
3	42	4.13	3.8–4.5	0.33	50	4.14	3.7–4.4	0.29
4	14	4.13	3.8–4.5	0.41	24	4.16	3.9–4.4	0.23
5	9	4.17	4.1–4.2	0.10	15	4.15	3.8–4.6	0.47
6	11	4.13	4.0–4.5	0.31	9	4.10	3.9–4.3	0.32
7	11	4.05	3.8–4.2	0.29	22	4.17	4.0–4.3	0.22
8	11	4.23	4.0–4.4	0.25	13	4.16	3.9–4.3	0.25
9	36	4.14	3.8–4.6	0.34	20	4.13	3.9–4.3	0.23
10	14	4.16	3.9–4.4	0.35	11	4.24	4.1–4.4	0.22

TABLE 16.—*Continued.*

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
11	10	4.23	4.1–4.5	0.25	8	4.16	3.9–4.4	0.34
12	13	4.17	3.9–4.3	0.28	14	4.10	3.8–4.3	0.29
13	26	4.19	4.0–4.5	0.24	15	4.18	4.0–4.4	0.23
14	10	4.08	3.6–4.2	0.37	6	4.28	4.1–4.5	0.27
15	6	4.15	4.0–4.3	0.21	5	4.24	4.1–4.4	0.23
16	32	4.25	4.0–4.5	0.25	32	4.24	3.8–4.5	0.35
17	6	4.25	4.1–4.5	0.33	8	4.33	4.2–4.4	0.14
18	5	4.38	4.3–4.5	0.22	9	4.36	4.1–4.6	0.33
19	7	4.11	3.8–4.4	0.50	9	4.30	4.0–4.5	0.28
20	6	3.98	3.8–4.1	0.23	4	4.00	3.9–4.1	0.16
21	6	3.98	3.8–4.2	0.29	9	3.94	3.6–4.2	0.33
22	15	3.88	3.7–4.0	0.17	18	3.87	3.7–4.2	0.31
23	19	3.96	3.7–4.2	0.22	10	3.95	3.7–4.1	0.32
24	5	4.00	3.9–4.1	0.20	4	4.00	3.9–4.2	0.28
25	20	3.95	3.7–4.2	0.25	22	3.97	3.7–4.3	0.28
26	6	3.95	3.8–4.1	0.21				
27	10	3.95	3.8–4.2	0.22	4	4.05	3.8–4.2	0.38
28	5	4.00	3.8–4.1	0.28	6	4.05	3.9–4.2	0.25
29	6	4.03	3.8–4.2	0.27	8	4.09	3.9–4.3	0.27
30	13	3.98	3.7–4.2	0.26	14	4.06	3.9–4.2	0.23
31	7	4.26	4.1–4.3	0.16	10	4.27	4.1–4.5	0.25
32	11	3.88	3.7–4.0	0.20	11	4.00	3.7–4.3	0.35
<i>Breadth of braincase</i>								
1	18	8.58	8.2–8.9	0.40	13	8.50	8.4–8.6	0.14
2	9	8.38	8.1–8.6	0.28	21	8.41	7.9–8.6	0.39
3	43	8.47	8.0–8.8	0.36	48	8.52	8.1–8.9	0.35
4	13	8.47	8.2–8.6	0.25	21	8.53	8.3–8.9	0.31
5	9	8.43	8.1–8.7	0.14	15	8.43	8.1–8.8	0.35
6	11	8.48	8.3–8.7	0.23	8	8.28	8.0–8.5	0.33
7	11	8.50	8.3–8.9	0.33	21	8.47	8.1–8.7	0.34
8	11	8.55	8.3–8.8	0.29	11	8.53	8.2–8.7	0.32
9	35	8.45	8.0–8.9	0.40	19	8.45	8.2–8.7	0.32
10	14	8.56	8.4–8.8	0.26	11	8.66	8.5–9.0	0.29
11	10	8.49	8.2–8.7	0.29	9	8.53	8.3–8.7	0.28
12	12	8.49	8.2–9.0	0.50	11	8.37	8.2–8.6	0.27
13	25	8.57	8.2–8.8	0.31	14	8.60	8.4–9.0	0.38
14	10	8.48	8.2–8.7	0.31	6	8.52	8.2–8.8	0.43
15	6	8.57	8.5–8.7	0.16	3	8.60	8.3–8.9	0.60
16	27	8.62	8.3–8.9	0.32	30	8.62	8.2–9.1	0.37
17	6	8.80	8.6–9.2	0.49	7	8.54	8.3–8.8	0.38
18	5	8.88	8.7–9.0	0.26	8	8.81	8.7–8.9	0.17
19	7	8.46	8.1–8.7	0.43	9	8.59	8.3–9.0	0.39
20	6	8.42	8.3–8.6	0.20	4	8.40	8.2–8.5	0.28
21	6	8.42	8.2–8.6	0.29	9	8.26	7.8–8.5	0.46

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
22	15	8.33	8.0–8.5	0.29	17	8.39	8.2–8.7	0.30
23	19	8.31	8.1–8.6	0.26	10	8.22	8.0–8.5	0.28
24	5	8.34	8.2–8.5	0.23	4	8.48	8.3–8.6	0.25
25	18	8.41	8.1–8.7	0.27	19	8.36	8.0–8.7	0.35
26	6	8.57	8.3–9.0	0.50				
27	10	8.48	8.1–8.9	0.40	5	8.58	8.4–8.9	0.38
28	5	8.44	8.2–8.7	0.36	5	8.74	8.5–8.9	0.36
29	6	8.40	8.1–8.7	0.47	8	8.49	8.2–8.7	0.39
30	12	8.54	8.4–8.7	0.26	13	8.65	8.4–8.9	0.32
31	7	8.63	8.2–8.9	0.44	10	8.71	8.2–8.9	0.48
32	11	8.36	8.1–8.8	0.39	8	8.33	8.0–8.5	0.33
<i>Depth of braincase</i>								
1	17	6.97	6.7–7.3	0.40	12	6.80	6.6–7.3	0.40
2	9	6.77	6.6–7.0	0.25	19	6.80	6.5–7.3	0.39
3	40	6.91	6.6–7.3	0.39	46	6.90	6.5–7.3	0.41
4	13	6.81	6.5–7.0	0.29	21	6.84	6.5–7.3	0.44
5	9	6.83	6.5–7.0	0.33	14	6.80	6.5–7.1	0.38
6	8	7.06	6.7–7.2	0.34	6	6.80	6.5–7.0	0.36
7	11	6.91	6.7–7.2	0.32	21	6.72	6.5–7.0	0.33
8	11	6.96	6.8–7.4	0.36	11	6.95	6.8–7.3	0.30
9	35	6.90	6.5–7.3	0.39	18	6.87	6.4–7.3	0.45
10	14	6.96	6.7–7.3	0.41	11	7.10	6.8–7.3	0.30
11	10	6.96	6.7–7.2	0.40	9	6.98	6.7–7.4	0.42
12	11	6.95	6.7–7.3	0.38	11	6.76	6.3–7.4	0.50
13	24	6.99	6.6–7.3	0.41	14	6.96	6.7–7.2	0.31
14	10	7.03	6.6–7.4	0.51	6	6.98	6.7–7.3	0.57
15	6	6.98	6.8–7.1	0.23	3	6.87	6.7–7.0	0.31
16	28	7.00	6.6–7.3	0.34	31	6.94	6.6–7.5	0.39
17	6	7.08	6.6–7.3	0.53	7	6.81	6.6–7.1	0.45
18	5	7.12	6.9–7.4	0.43	9	7.17	6.9–7.5	0.40
19	7	6.90	6.7–7.2	0.37	9	6.84	6.7–7.0	0.41
20	6	6.92	6.7–7.2	0.39	4	6.85	6.6–7.0	0.38
21	6	6.92	6.8–7.1	0.23	8	6.84	6.6–7.3	0.48
22	15	6.89	6.5–7.2	0.46	18	6.79	6.5–7.1	0.34
23	19	6.83	6.5–7.2	0.37	10	6.79	6.6–7.1	0.37
24	5	6.80	6.4–7.0	0.57	3	6.67	6.6–6.7	0.12
25	17	6.87	6.4–7.3	0.45	19	6.78	6.3–7.0	0.34
26	5	6.88	6.7–7.0	0.26				
27	10	6.91	6.6–7.4	0.52	5	6.98	6.8–7.2	0.36
28	5	6.98	6.8–7.2	0.41	5	6.96	6.4–7.2	0.67
29	6	6.85	6.5–7.3	0.52	8	6.84	6.6–7.1	0.30
30	12	6.87	6.5–7.1	0.31	10	6.89	6.5–7.3	0.47
31	7	6.96	6.7–7.1	0.36	10	6.94	6.7–7.2	0.27
32	11	6.68	6.3–7.3	0.64	8	6.75	6.4–7.0	0.52

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
<i>Length of maxillary tooththrow</i>								
1	18	7.46	7.2–7.7	0.29	15	7.62	7.4–7.9	0.33
2	9	7.18	6.8–7.7	0.54	21	7.38	7.0–7.7	0.38
3	41	7.26	6.8–7.7	0.34	47	7.36	6.9–7.8	0.37
4	11	7.26	7.0–7.5	0.34	24	7.35	7.0–7.7	0.38
5	8	7.25	7.0–7.4	0.26	15	7.40	7.3–7.6	0.17
6	11	7.29	7.1–7.6	0.30	9	7.21	6.9–7.6	0.41
7	10	7.10	6.8–7.4	0.41	20	7.19	6.9–7.5	0.30
8	11	7.26	7.1–7.5	0.24	12	7.28	7.0–7.5	0.30
9	37	7.24	6.9–7.6	0.35	18	7.27	6.8–7.6	0.36
10	15	7.25	7.1–7.4	0.20	11	7.36	6.9–7.8	0.49
11	10	7.27	7.0–7.5	0.35	10	7.24	7.0–7.4	0.29
12	13	7.26	7.0–7.5	0.28	14	7.34	7.2–7.5	0.23
13	25	7.23	6.8–7.6	0.39	15	7.31	7.0–7.6	0.33
14	10	7.17	6.9–7.5	0.40	6	7.15	7.1–7.3	0.17
15	4	7.25	7.0–7.5	0.48	5	7.40	7.2–7.7	0.37
16	32	7.57	7.3–8.0	0.36	31	7.72	7.4–8.3	0.47
17	6	7.62	7.5–7.8	0.23	7	7.66	7.4–7.9	0.34
18	5	7.76	7.6–7.9	0.23	9	7.87	7.5–8.2	0.40
19	7	7.57	7.4–7.9	0.36	9	7.60	7.5–7.9	0.41
20	6	6.92	6.8–7.0	0.15	4	7.10	6.8–7.4	0.49
21	6	6.93	6.7–7.2	0.35	9	7.01	6.7–7.4	0.49
22	16	6.83	6.4–7.2	0.33	18	6.88	6.5–7.2	0.45
23	19	7.03	6.7–7.4	0.40	10	7.09	6.9–7.2	0.22
24	4	6.95	6.8–7.1	0.26	4	7.18	6.9–7.4	0.41
25	19	6.85	6.4–7.3	0.44	22	6.97	6.7–7.3	0.36
26	6	6.82	6.7–7.0	0.23				
27	9	6.87	6.6–7.1	0.37	5	7.00	6.8–7.1	0.25
28	5	7.10	6.8–7.4	0.45	6	7.15	6.9–7.3	0.33
29	6	7.00	6.8–7.1	0.25	8	7.14	6.9–7.4	0.34
30	13	6.99	6.6–7.2	0.35	13	7.15	7.0–7.4	0.24
31	7	7.50	7.4–7.7	0.23	9	7.51	7.3–7.7	0.25
32	10	6.91	6.6–7.2	0.64	11	7.15	6.7–7.5	0.44
<i>Length of mandibular tooththrow</i>								
1	18	7.85	7.6–8.0	0.25	15	7.97	7.7–8.3	0.40
2	9	7.63	7.4–8.2	0.53	21	7.80	7.4–8.1	0.37
3	41	7.68	7.2–8.1	0.33	46	7.75	7.4–8.2	0.32
4	11	7.65	7.4–8.0	0.37	24	7.71	7.4–8.0	0.36
5	9	7.63	7.5–7.8	0.22	15	7.75	7.6–7.9	0.17
6	11	7.73	7.5–8.0	0.30	9	7.51	7.3–7.8	0.32
7	10	7.56	7.2–7.9	0.44	20	7.60	7.2–7.9	0.32
8	11	7.69	7.5–7.8	0.21	13	7.68	7.3–7.9	0.39
9	37	7.69	7.4–8.0	0.33	19	7.66	7.1–7.9	0.41
10	15	7.63	7.4–7.9	0.29	11	7.71	7.3–8.2	0.53

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
11	9	7.68	7.4–7.9	0.33	9	7.67	7.4–7.9	0.33
12	13	7.71	7.4–7.9	0.31	13	7.74	7.6–7.9	0.17
13	26	7.70	7.3–8.1	0.43	15	7.74	7.4–8.0	0.32
14	10	7.64	7.4–7.8	0.34	6	7.50	7.4–7.6	0.18
15	5	7.70	7.5–7.9	0.37	6	7.73	7.6–8.1	0.37
16	32	8.02	7.6–8.4	0.38	31	8.13	7.7–8.7	0.49
17	6	8.05	7.9–8.2	0.21	8	8.08	7.9–8.3	0.26
18	5	8.20	8.0–8.3	0.25	8	8.33	8.0–8.7	0.44
19	7	8.10	8.0–8.3	0.26	9	7.94	7.5–8.4	0.63
20	6	7.32	7.2–7.5	0.23	4	7.48	7.3–7.6	0.25
21	6	7.35	7.1–7.8	0.52	9	7.37	7.1–7.7	0.47
22	16	7.24	7.0–7.5	0.24	18	7.26	6.8–7.6	0.45
23	19	7.43	7.1–7.7	0.41	10	7.41	7.2–7.6	0.24
24	5	7.30	7.2–7.5	0.28	4	7.50	7.3–7.6	0.28
25	16	7.29	6.8–7.7	0.46	22	7.33	6.9–7.8	0.40
26	6	7.27	7.1–7.6	0.35				
27	10	7.26	7.0–7.4	0.27	4	7.33	7.0–7.5	0.47
28	5	7.46	7.1–7.7	0.52	5	7.50	7.3–7.6	0.25
29	6	7.38	7.1–7.5	0.37	8	7.48	7.4–7.8	0.30
30	13	7.36	7.0–7.6	0.37	14	7.51	7.3–7.8	0.29
31	7	8.03	7.9–8.2	0.25	9	7.93	7.8–8.1	0.20
32	11	7.32	7.0–7.5	0.36	11	7.48	7.2–7.8	0.41
Width across molars								
1	18	5.51	5.3–5.7	0.23	15	5.47	5.2–5.7	0.32
2	9	5.50	5.2–5.8	0.40	21	5.60	5.3–5.8	0.31
3	41	5.53	5.2–5.8	0.33	46	5.58	5.4–5.7	0.32
4	14	5.48	5.3–5.7	0.28	23	5.54	5.3–6.0	0.21
5	9	5.54	5.4–5.8	0.28	14	5.59	5.4–5.8	0.25
6	10	5.48	5.2–5.7	0.30	9	5.48	5.0–5.7	0.40
7	10	5.47	5.2–5.8	0.39	20	5.42	5.1–5.8	0.34
8	11	5.61	5.3–6.0	0.38	11	5.55	5.3–5.7	0.24
9	36	5.50	5.2–5.9	0.33	16	5.41	5.0–5.7	0.36
10	14	5.53	5.3–5.8	0.27	11	5.51	5.2–5.7	0.28
11	10	5.55	5.3–5.8	0.29	10	5.55	5.3–5.8	0.29
12	13	5.48	5.3–5.6	0.22	14	5.46	5.3–5.7	0.26
13	25	5.55	5.3–5.8	0.27	15	5.57	5.3–5.7	0.25
14	9	5.43	5.3–5.5	0.17	6	5.42	5.1–5.7	0.43
15	4	5.50	5.4–5.6	0.23	5	5.64	5.4–5.7	0.27
16	32	5.71	5.4–6.0	0.30	32	5.71	5.4–6.0	0.35
17	6	5.70	5.5–5.8	0.25	8	5.68	5.4–5.8	0.26
18	5	5.64	5.5–5.8	0.23	9	5.77	5.7–5.9	0.14
19	7	5.70	5.5–5.9	0.31	9	5.62	5.3–5.9	0.40
20	6	5.47	5.1–5.6	0.37	4	5.45	5.2–5.7	0.42

TABLE 16.—Continued.

Sample number	Males				Females			
	N	Mean	Range	2SD	N	Mean	Range	2SD
22	16	5.26	5.1–5.5	0.29	18	5.23	4.9–5.6	0.37
23	18	5.28	4.9–5.6	0.34	10	5.31	5.1–5.6	0.30
24	4	5.30	5.1–5.5	0.33	4	5.45	5.2–5.7	0.48
25	20	5.19	4.8–5.4	0.33	22	5.32	5.0–5.7	0.30
26	6	5.28	5.1–5.7	0.43				
27	10	5.13	4.9–5.5	0.33	5	5.28	5.1–5.5	0.33
28	5	5.30	4.9–5.7	0.52	6	5.33	5.2–5.5	0.24
29	6	5.35	5.2–5.5	0.21	8	5.40	5.3–5.5	0.15
30	13	5.24	5.1–5.4	0.21	13	5.39	5.2–5.6	0.34
31	7	5.84	5.7–6.0	0.20	8	5.76	5.7–5.9	0.15
32	10	5.30	5.0–5.4	0.30	11	5.36	4.9–5.7	0.47
<i>Mandibular length</i>								
1	18	14.16	13.5–14.7	0.65	15	14.29	14.0–14.7	0.42
2	9	13.56	13.2–14.1	0.57	22	13.78	13.1–14.4	0.64
3	42	13.60	12.9–14.3	0.53	47	13.81	13.3–14.3	0.50
4	12	13.61	13.2–14.1	0.54	24	13.73	13.2–14.3	0.62
5	9	13.68	13.3–14.0	0.48	15	13.85	13.6–14.3	0.40
6	11	13.73	13.6–14.1	0.31	9	13.44	13.2–13.8	0.44
7	12	13.43	12.9–13.9	0.57	21	13.59	12.7–14.1	0.62
8	11	13.69	13.5–14.0	0.30	12	13.76	13.3–14.3	0.61
9	36	13.56	12.9–14.2	0.57	20	13.65	12.9–14.3	0.55
10	14	13.60	13.3–13.9	0.42	11	13.80	12.9–14.5	0.84
11	9	13.66	13.5–14.0	0.39	7	13.57	13.2–13.8	0.38
12	12	13.65	13.0–14.0	0.56	10	13.74	13.5–14.3	0.44
13	25	13.71	13.3–14.4	0.56	15	13.73	13.5–14.0	0.34
14	10	13.54	12.8–14.0	0.76	6	13.55	13.3–13.7	0.35
15	6	13.53	13.1–13.8	0.52	6	13.67	13.3–14.3	0.72
16	33	14.22	13.7–14.6	0.50	31	14.43	13.5–15.2	0.73
17	5	14.32	14.1–14.6	0.46	7	14.37	14.2–14.7	0.34
18	5	14.62	14.3–14.8	0.38	8	14.81	14.3–15.2	0.57
19	7	14.29	13.9–14.7	0.55	9	14.28	13.7–15.0	0.82
20	6	12.88	12.7–13.2	0.43	4	13.15	12.8–13.4	0.50
21	6	13.15	12.8–14.0	0.87	9	13.03	12.5–13.7	0.78
22	15	12.95	12.6–13.3	0.47	16	12.93	12.7–13.5	0.46
23	19	13.06	12.8–13.4	0.41	10	13.09	12.9–13.4	0.39
24	5	13.08	12.8–13.3	0.38	4	13.28	12.8–13.7	0.89
25	18	12.89	12.2–13.3	0.54	19	13.06	12.5–13.7	0.64
26	6	12.83	12.7–13.0	0.27				
27	10	12.81	12.2–13.6	0.77	3	13.10	12.8–13.5	0.72
28	5	13.12	12.6–13.7	0.92	6	13.25	12.9–13.5	0.49
29	6	12.90	12.5–13.1	0.49	8	13.29	12.9–13.8	0.62
30	12	13.10	12.5–13.5	0.55	13	13.35	13.0–13.7	0.38
31	7	14.41	14.1–14.7	0.41	10	14.40	14.1–14.6	0.28
32	11	13.01	12.6–13.6	0.52	11	13.35	12.8–14.1	0.72

Pelage coloration.—Overall, specimens from the Tres Mariás Islands (1), Jamaica (31), and the west coasts of Ecuador and Perú (16-19) average paler, and those from Amazonian South America (21-30) and Trinidad (32) average slightly darker in color than do specimens from other samples (2-15, 20). There is, however, tremendous variation in color, probably because molt is not highly synchronized and specimens with pale, worn pelage and dark, unworn pelage can be collected from the same population during certain times of the year.

TABLE 17.—*Results of four SS-STP tests of geographic variation in Glossophaga soricina. Vertical lines to the right of sample means connect maximally nonsignificant subsets at the 0.05 probability level for length of forearm, greatest length of skull, width across molars, and mandibular length. See text and Figures 21–22 for key to sample numbers.*

Sample number	Males		Sample number	Females	
	Mean	Results SS-STP		Mean	Results SS-STP
<i>Length of forearm</i>					
18	36.74		18	37.96	
19	36.60		19	37.48	
31	36.51		1	37.26	
1	36.42		31	37.18	
17	36.13		17	37.04	
4	35.85		2	36.39	
5	35.71		16	36.29	
6	35.65		32	36.26	
8	35.58		5	36.23	
12	35.46		4	36.16	
3	35.33		3	36.00	
2	35.31		20	35.93	
13	35.11		10	35.79	
10	35.01		29	35.71	
29	34.98		12	35.70	
26	34.98		7	35.67	
16	34.96		8	35.60	
9	34.89		13	35.51	
11	34.80		9	35.39	
7	34.78		11	35.38	
14	34.77		14	35.30	
30	34.73		6	35.29	
22	34.71		24	35.10	
32	34.69		25	35.09	
15	34.57		30	34.93	
23	34.41		15	34.87	
28	34.32		27	34.82	
21	34.23		28	34.63	
24	34.22		23	34.35	
25	34.08		22	34.15	
20	33.93		21	33.80	
27	33.50				

Qualitative cranial characters (Table 5).—Pterygoid alae were well developed in 79.3 percent and modestly developed in 17.3 percent of the *Glossophaga soricina* examined by me, being absent in only 28 of 811 (3.5 percent) individuals. Specimens from northern Colombia (14) always have well-developed pterygoid alae, whereas those from Oaxaca (7), western Perú (17-18), southeastern Perú (24), Brazil (25-28), Bolivia (29), and Paraguay (30) tend to have poorly developed pterygoid alae or lack them entirely.

The presphenoid ridge is high and complete throughout (96.1 percent) or moderately developed (3.4 percent) in *G. soricina*, with only four of 825 (0.5 percent) specimens having a presphenoid ridge that is flattened subterminally. There is little geographic variation in this character.

TABLE 17.—Continued.

Sample number	Males			Sample number	Females		
	Mean	Results	SS-STP		Mean	Results	SS-STP
<i>Greatest length of skull</i>							
18	22.60			18	22.84		
17	22.32			16	22.21		
31	22.21			31	22.15		
16	22.15			17	22.11		
1	21.96			1	22.01		
19	21.94			19	21.94		
6	21.55			15	21.73		
12	21.46			10	21.55		
11	21.43			2	21.49		
4	21.42			5	21.45		
13	21.42			12	21.45		
5	21.40			3	21.44		
8	21.39			8	21.42		
10	21.35			13	21.34		
3	21.27			4	21.32		
15	21.23			11	21.26		
2	21.19			9	21.25		
14	21.15			14	21.25		
9	21.15			7	21.22		
7	21.05			6	21.03		
28	20.80			32	20.89		
21	20.60			28	20.77		
30	20.51			30	20.76		
24	20.50			20	20.75		
23	20.49			24	20.70		
32	20.48			29	20.56		
22	20.35			27	20.44		
20	20.30			23	20.38		
29	20.23			21	20.29		
25	20.19			25	20.26		
27	20.06			22	20.25		
26	19.98						

The angle of projection of the upper incisors is noticeably procumbent (82.3 per-cent), particularly in specimens from the Tres Marías Islands (1), west-central México (5), Jamaica (31), western Colombia (15), and southwestern Perú (18) where all individuals possess this character. Moderately procumbent upper in-cisors occurred in 17.4 percent of the specimens examined, especially those from the Magdalena River Valley (20), southeastern Perú (24), Paraguay (30), and east-ern Brazil (28). Only three of 801 (0.4 percent) specimens, a female from Hidalgo (6) and a male from Paraguay (30) and one from northeastern Brazil (26), have upper incisors that are not noticeably procumbent.

The upper incisors are unequal (98.6 percent) in bulk in *G. soricina*, and there is little geographic variation in this character. Of 800 specimens examined by me,

TABLE 17.—Continued.

Males			Females		
Sample number	Mean	Results SS-STP	Sample number	Mean	Results SS-STP
Width across molars					
31	5.84		18	5.77	
16	5.71		31	5.76	
17	5.70		16	5.70	
19	5.70		17	5.68	
18	5.64		15	5.64	
8	5.61		19	5.62	
13	5.55		2	5.60	
11	5.55		5	5.59	
5	5.54		3	5.58	
10	5.53		13	5.57	
3	5.53		11	5.55	
1	5.51		8	5.55	
9	5.50		4	5.54	
15	5.50		10	5.51	
2	5.50		6	5.48	
6	5.48		1	5.47	
4	5.48		12	5.46	
12	5.48		20	5.45	
7	5.47		24	5.45	
20	5.47		7	5.42	
14	5.43		14	5.42	
21	5.35		9	5.41	
29	5.35		29	5.40	
28	5.30		30	5.39	
32	5.30		32	5.36	
24	5.30		28	5.33	
26	5.28		25	5.32	
23	5.28		23	5.31	
22	5.26		27	5.28	
30	5.24		21	5.26	
25	5.19		22	5.23	
27	5.13				

only seven (0.9 percent) had upper incisors that were subequal in bulk and only four (0.5 percent) had equal upper incisors.

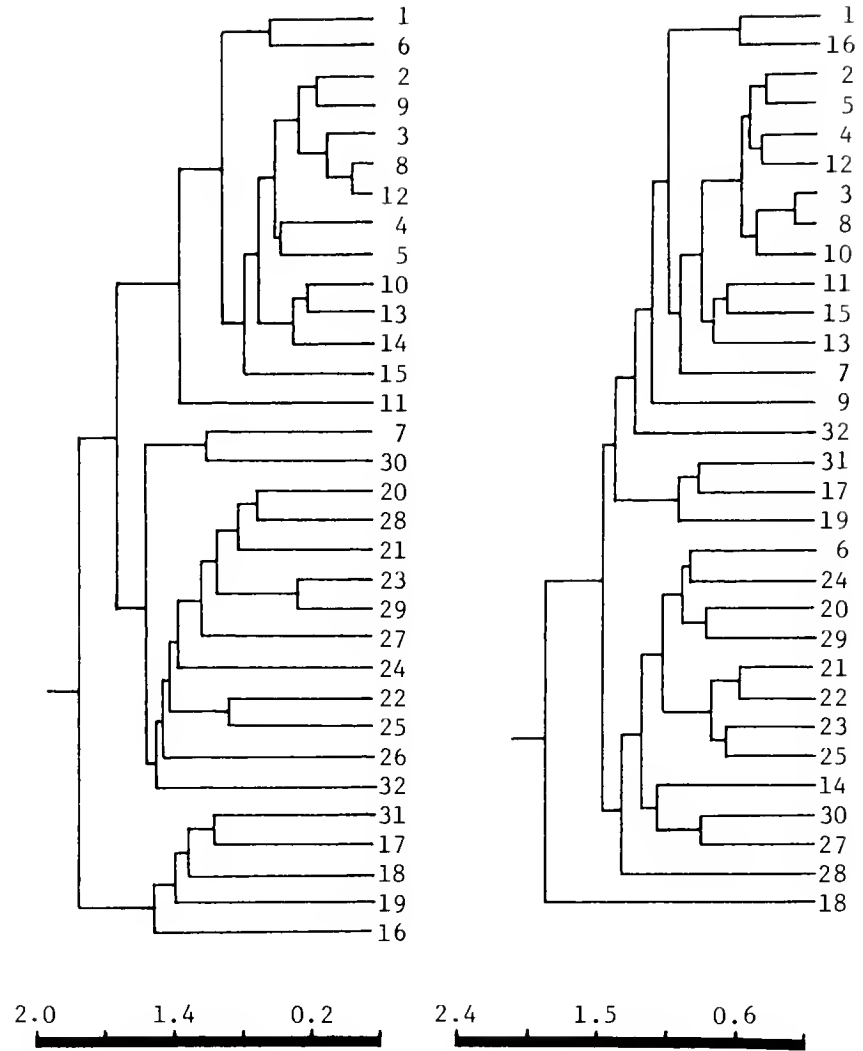
The lower incisors usually are large and in contact (95.7 percent). In 34 of 806 (4.2 percent) specimens, they are medium in size and have small gaps between the teeth, particularly in individuals from Paraguay (30). One male (KU 103259) from Honduras has lower incisors that are peglike and paired, similar to the condition found in *G. commissarisi*, but in all other characters this specimen most closely resembles *G. soricina*.

The upper premolars are unequal (98.2 percent) in bulk because in P4 the posterolingual cingulum is greatly developed. Fourteen of 835 (1.7 percent) specimens have upper premolars that are subequal in bulk, and seven of these are from western Ecuador (16). Only one specimen (0.1 percent) of those examined possess upper premolars that are equal in bulk.

TABLE 17.—Continued.

Sample number	Males			Sample number	Females		
	Mean	Results	SS-STP		Mean	Results	SS-STP
<i>Mandibular length</i>							
18	14.62			18	14.81		
31	14.41			16	14.43		
17	14.32			31	14.40		
19	14.29			17	14.37		
16	14.22			1	14.29		
1	14.16			19	14.28		
6	13.73			5	13.85		
13	13.71			3	13.81		
8	13.69			10	13.80		
5	13.68			2	13.78		
11	13.66			8	13.76		
12	13.65			12	13.74		
4	13.61			13	13.73		
3	13.60			4	13.73		
10	13.60			15	13.67		
9	13.56			9	13.65		
2	13.56			7	13.59		
14	13.54			11	13.57		
15	13.53			14	13.55		
7	13.43			6	13.44		
21	13.15			32	13.35		
28	13.12			30	13.35		
30	13.10			29	13.29		
24	13.08			24	13.28		
23	13.06			28	13.25		
32	13.01			20	13.15		
22	12.95			27	13.10		
29	12.90						

FIG. 23.—Distance phenograms for 32 samples of *Glossophaga soricina*. Phenograms were computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages for males (left) and females (right). The cophenetic coefficient of correlation for the phenogram for males is 0.781 and for females is 0.770. See Figures 21-22 and text for key to samples.



Basisphenoid pits are shallow (39.9 percent) or moderately deep (48.0 percent) in *G. soricina*, being shallow most often in specimens from México, Belize, Guatamala, and El Salvador (1-10). Basisphenoid pits were deep in 12.1 percent of the bats examined, particularly in some specimens from Honduras (11), Jamaica (31), Costa Rica, Panamá, northern and western Colombia (13-15), northwestern Perú (17,19), and Brazil (25-28).

The slope from rostrum to braincase usually is gradual (72.0 percent) in *G. soricina*. However, 11.9 percent of the specimens examined, especially those from northern, west-central, and southern México (2-3, 5, 8) Nicaragua (12), Jamaica (31), and western Perú (17-19) had a continuous slope from rostrum to braincase, whereas 15.8 percent had a moderate rostral slope, the latter being primarily from Oaxaca (7), Costa Rica and western Panamá (13), the Magdalena River Valley (20), the Guianas (22), Bolivia (29), Paraguay (30), and Brazil (25-28). Two of 847 (0.2 percent) specimens, a female from Oaxaca (7) and a male from Amazonas, Brazil (25), have an abrupt rostral slope.

Posterior palatine processes were poorly (50.1 percent), moderately (25.6 percent), or greatly (14.3 percent) developed in *G. soricina*, being absent in 10.0 percent of the specimens examined. Postpalatal processes are absent most frequently in individuals from northwestern México (2), Honduras (11), western Ecuador (16), southwestern Perú (18), and Amazonian Ecuador and Perú (23). Well-

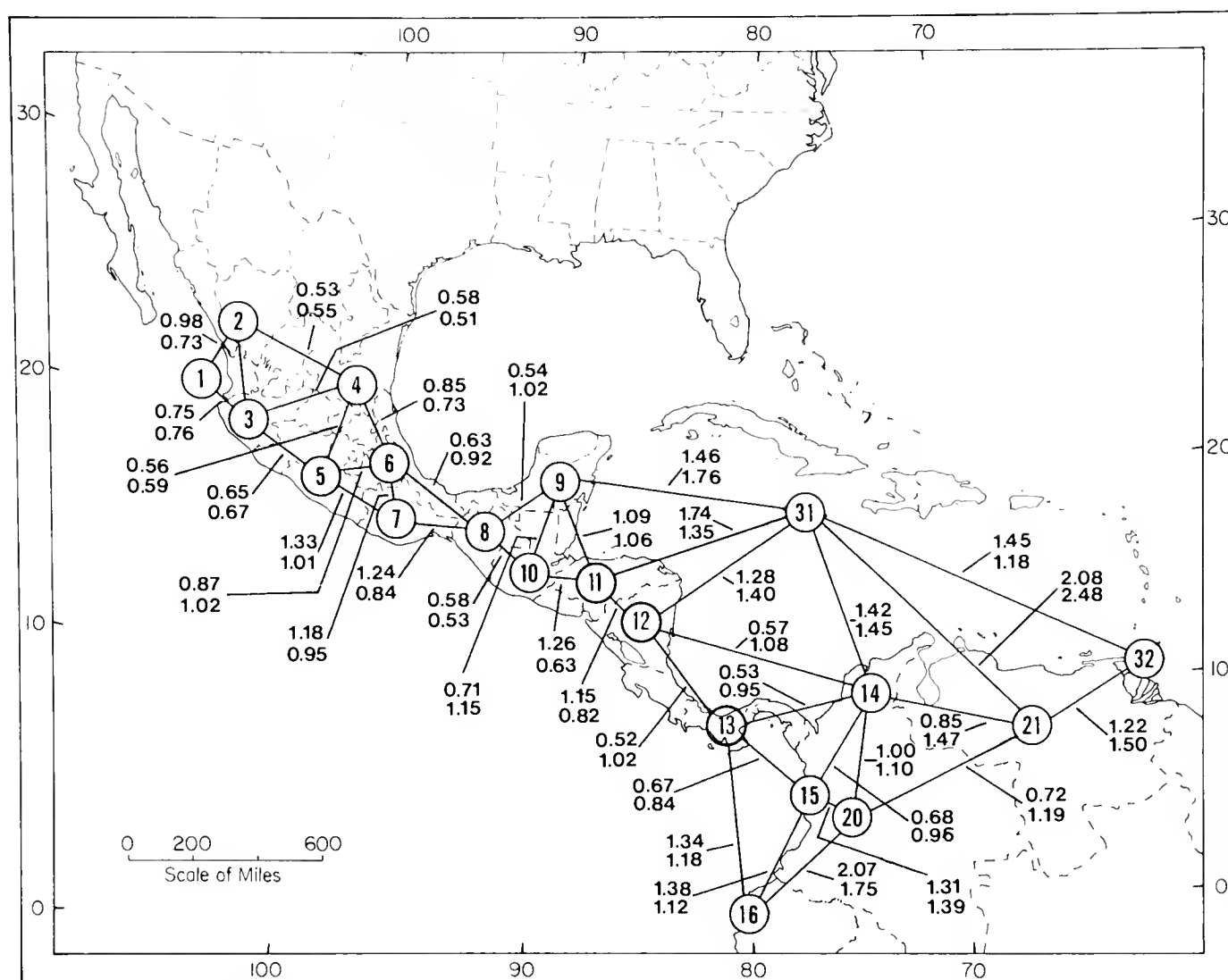


FIG. 24.—Selected distance coefficients among some of 32 samples of *Glossophaga soricina* from North America and northern South America. Coefficients are from distance matrices for males (above) and females (below). See Figures 21-22 and text for key to samples.

developed postpalatal processes are most common in bats from Oaxaca (7), Guatamala and El Salvador (10), Jamaica (31), northwestern and southeastern Perú (17, 24), and Paraguay (30).

Multivariate Analysis

The external and cranial measurements, color, and qualitative cranial characters were analyzed using the NT-SYS programs, and phenograms were computed for both distance and correlation matrices to display phenetic relationships of males and females of *Glossophaga soricina*. Distance phenograms are presented herein (Fig. 23), and selected distance coefficients between samples for each sex are included (Figs. 24-25).

The distance phenogram for male *G. soricina* indicates that the samples cluster into three major groups. Individuals from Jamaica (31) and the west coasts of Ecuador and Perú (16-19) form a group that is characterized by pale pelage and large size (both externally and cranially). The second phenetically distinct group is comprised of specimens from Oaxaca (7), South America east of the Andes (21-30),

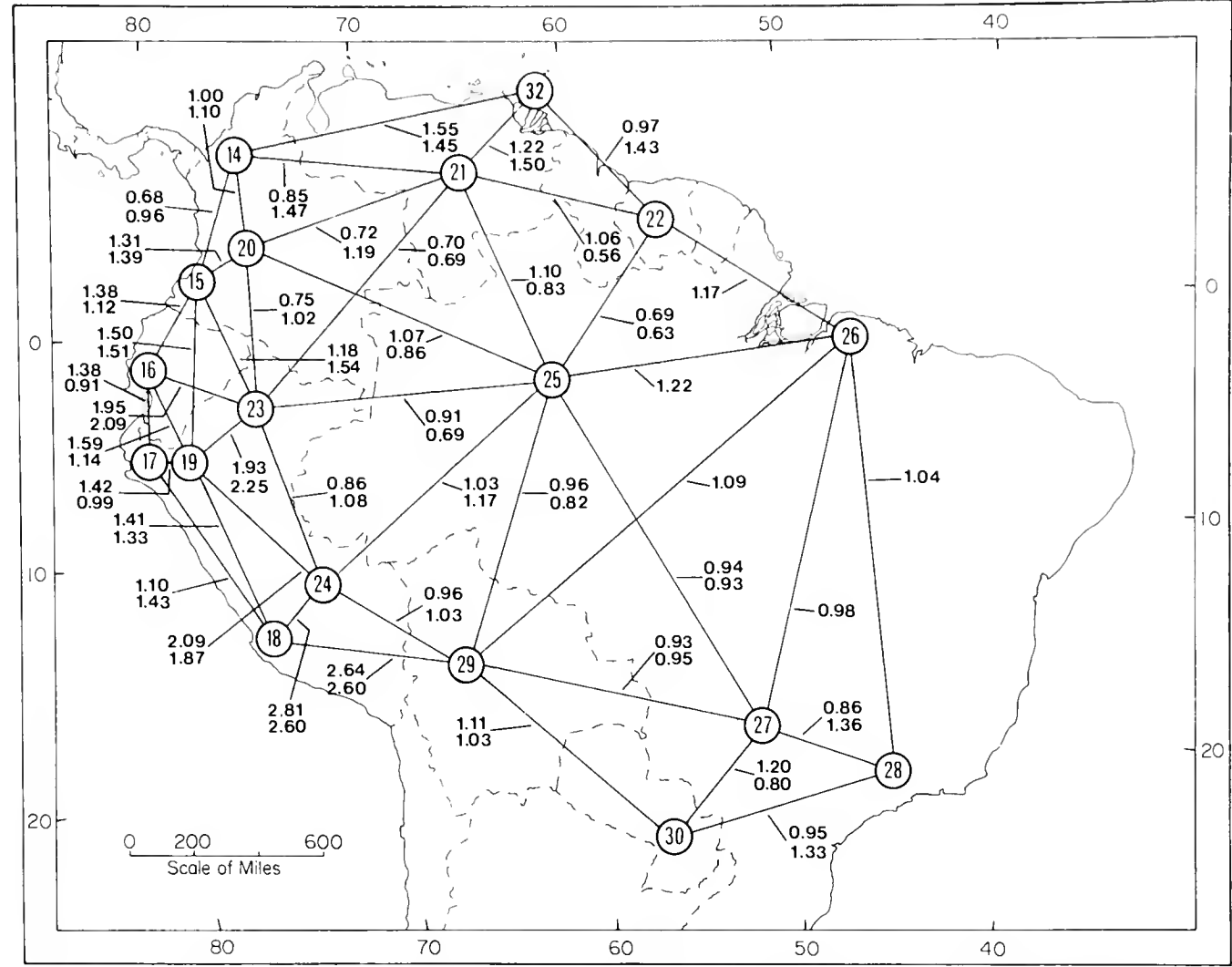
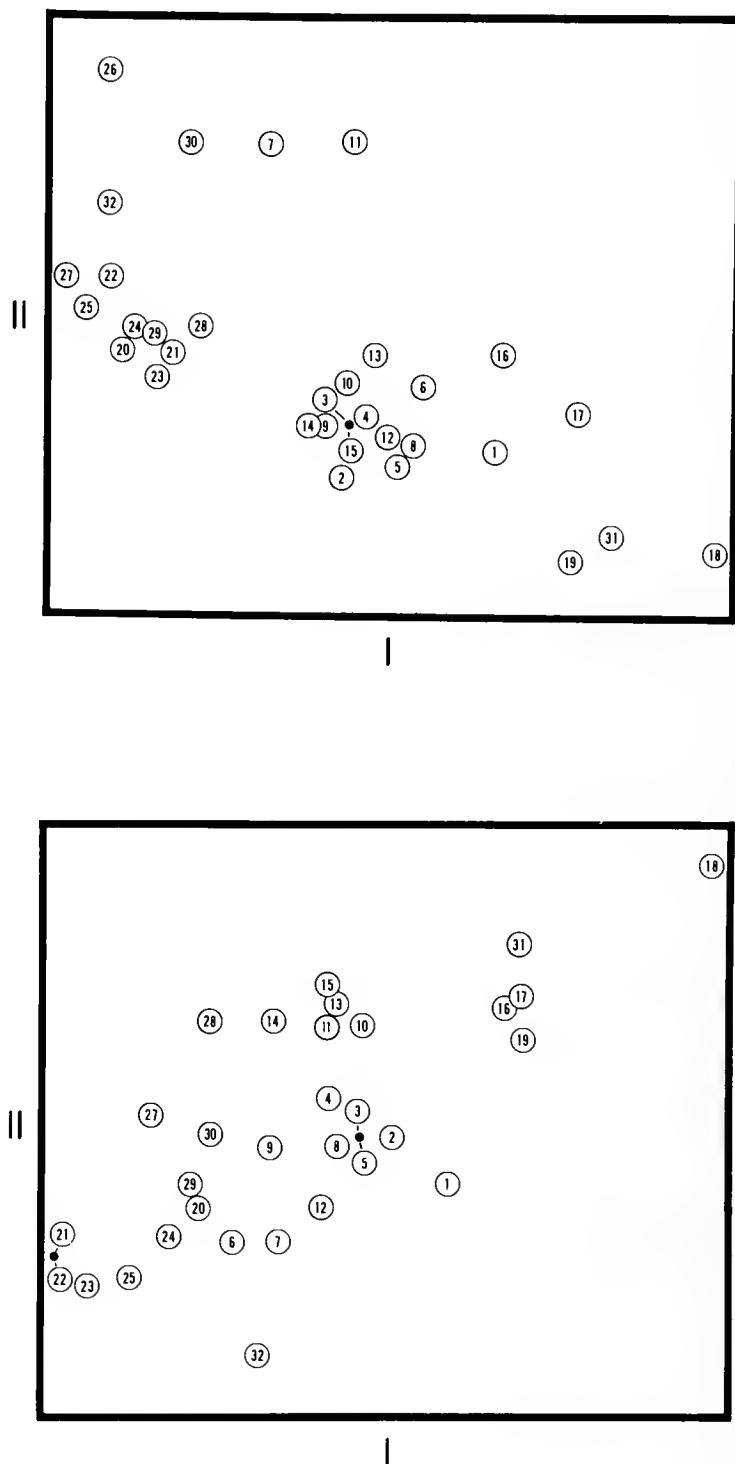


FIG. 25.—Selected distance coefficients among some of 32 samples of *Glossophaga soricina* from South America. Coefficients are from distance matrices for males (above) and females (below). See Figures 21-22 and text for key to samples.

Trinidad (32), and the upper Magdalena River Valley (20). This group is characterized by small size overall and dark pelage. Specimens from Middle America, except Oaxaca (1-6, 8-13), and northern and western Colombia (14-15) represent the third group that is intermediate in size and pelage coloration relative to the two groups mentioned above.

The distance phenogram for female *G. soricina* shows the samples clustering into three groups that are similar to those discussed for males. Specimens from southwestern Perú (18) form a phenetically distinct group that is characterized by its massive external and cranial dimensions. The second group, which is distinguished by small size and dark pelage, includes individuals from eastern México (6), northern Colombia (14), and South America east of the Andes (21-30). Bats from most of Middle America except eastern México (1-5, 7-13), western Colombia (15), Jamaica (31), Trinidad (32), and western Ecuador and northwestern Perú (16-17, 19) comprise the third phenetically distinct group. This group is recognizable because its members are relatively pale in pelage color and intermediate in size between the groups discussed above. The relatively large specimens from

FIG. 26.—Two-dimensional plots for 32 samples of *Glossophaga soricina*. Component I plotted against component II for males (top) and females (bottom). See Figures 21-22 and text for key to samples.



Jamaica (31) and northwestern Perú (17, 19), however, are phenetically distinct from the populations that constitute the remainder of this third group.

The first four principal components were computed from the correlation matrix among the 26 characters of the 32 samples based on the matrix of correlation among characters for both males and females. These four components combine to express 76.4 percent of phenetic variation in males and 75.6 percent in females. The amount of phenetic variation represented on the first four principal components for males and females, respectively, was 57.1 and 52.7 for component I, 7.6 and 9.8 for component II, 6.1 and 7.4 for component III, and 5.6 and 5.7 for component IV. Two-dimensional plots of principal components I-II are presented for both sexes (Fig. 26), and characters with loadings above 0.60 (or below -0.60) on any of the first four principal components are shown in Table 18.

TABLE 18.—*Factor loadings for 26 characters examined in Glossophaga soricina. Only loadings above 0.600 (or below -0.600) on the first four principal components are shown (males above, females below).*

Character	I	II	III	IV
Length of forearm	0.916			
	0.940			
Length of third metacarpal	0.942			
	0.928			
Length of fourth metacarpal	0.946			
	0.914			
Length of fifth metacarpal	0.935			
	0.896			
Greatest length of skull	0.922			
	0.956			
Condylobasal length	0.931			
	0.965			
Zygomatic breadth	0.831			
	0.795			
Length of rostrum	0.925			
	0.968			
Mastoid breadth	0.798			
	0.845			
Interorbital breadth	0.813			
	0.836			
Breadth of braincase	0.652			
		0.613		
Depth of braincase			-0.633	
		0.678		
Length of maxillary toothrow	0.916			
	0.942			
Length of mandibular toothrow	0.925			
	0.951			
Width across molars	0.837			
	0.875			
Mandibular length	0.943			
	0.970			
Pelage coloration	-0.730			
Pterygoid alae			-0.720	
			-0.632	
Presphenoid ridge				-0.635
Lower incisors		-0.793		
				0.850
Upper incisor angle				
			0.635	
Upper incisor size		0.778		

TABLE 18.—*Factor loadings for 26 characters examined in Glossophaga soricina. Only loadings above 0.600 (or below -0.600) on the first four principal components are shown (males above, females below).*

Character	I	II	III	IV
Basisphenoid pits				-0.610
P3:P4 bulk				
Rostral slope	-0.666			
	-0.754			
Postpalatal processes			-0.610	

OTUs of males and females of *G. soricina* on the right-hand side of component I are larger than average for the species in external and cranial dimensions; this includes specimens from the Tres Marías Islands (1), western Ecuador and Perú (16-19), and Jamaica (31). Those to the left-hand side of component I are from South America east of the Andes (21-30), Trinidad (32), and the upper Magdalena River Valley (20), and are smaller both externally and cranially. Little can be said about component II in that few characters load heavily on it. Likewise, components III and IV do not explain much of the total phenetic variation exhibited in *G. soricina*, and, therefore, are not figured.

Taxonomic Conclusions

Patterns of geographic variation and the disjunct nature of the insular populations indicate that there are five well-defined subspecies of *Glossophaga soricina*. Bats from Jamaica, to which the trinomial *Glossophaga soricina antillarum* Rehn applies, are large externally and cranially. Furthermore, owing to its isolated geographic status, it is doubtful that individuals of this race interbreed with those from the Central American mainland. Another insular race, *Glossophaga soricina mutica* Merriam, occupies the Tres Marías Islands. Individuals of this subspecies also are larger than those of the adjacent Mexican mainland both externally and cranially. A third race, characterized by moderate size in external and cranial dimensions, occurs from northern México (Sonora in the west and Tamaulipas in the east, but excluding much of the Mexican Plateau) southeastward through Middle America to the lowlands of western and northern Colombia. The name *Glossophaga soricina handleyi* Webster and Jones applies to this subspecies. Specimens from South America east of the Andes southward to northern Argentina and Paraguay represent another distinct race, *Glossophaga soricina soricina* Pallas, that is small in all external and cranial measurements and dark in pelage coloration. *G. s. soricina* also occupies the Maracaibo Basin and most of the Magdalena

River Valley from Cundinamarca southward. Only along the Magdalena River Valley does *G. s. soricina* intergrade with *G. s. handleyi*. The fifth subspecies, to which the name *Glossophaga soricina valens* Miller applies, occurs along the Pacific versant of Ecuador and Perú. This race, which is characterized by large size and pale pelage, also has invaded Amazonas, Perú, along xeric portions of the Río Marañón. Although *G. s. valens* and *G. s. soricina* both occur in Amazonas, they are essentially parapatric in distribution, and intergradation between them is not evident in specimens examined by me.

Glossophaga soricina antillarum Rehn

1902a. *Glossophaga soricina antillarum* Rehn, Proc. Nat. Acad. Sci. Philadelphia, 54:37, 23 April.

Holotype.—Adult female, skin (in alcohol) and skull, ANSP 6618 (but see Remarks), from Port Antonio, St. Thomas, Jamaica; obtained on 30 December 1890 by J. P. Moore, no original number. Holotype examined; pelage faded and zygoma damaged, but specimen otherwise in excellent condition.

Measurements of the holotype.—Length of forearm, 37.1; greatest length of skull, 22.3; condylobasal length, 20.6; mastoid breadth, 9.1; interorbital breadth, 4.4; length of maxillary toothrow, 7.7; length of mandibular toothrow (c-m3), 8.0.

Distribution.—Known certainly only from Jamaica (Fig. 27), but see Remarks.

Comparisons.—This race is characterized by large size, both externally and cranially (Table 16); a gradually sloping rostrum; extremely procumbent upper incisors; deep basisphenoid pits; well-developed postpalatal processes; and zygoma that converge anteriorly. The pelage of *G. s. antillarum* is paler than that of *G. s. handleyi* and *G. s. soricina*. The most trenchant characters, however, are large size and isolated geographic distribution; specimens of *G. s. antillarum*, *G. s. mutica*, and *G. s. valens* are difficult to distinguish by size alone.

Remarks.—Rehn (1902a) selected ANSP 6619 as the holotype of *G. s. antillarum*, the museum number 6619 being inscribed on the specimen label. However, the jar in which the bat is stored is labeled 6618 and ANSP 6618 is noted as the holotype in the ANSP catalogue. Koopman (1976) first discovered this discrepancy; ANSP 6619 is an *Artibeus*, not a *Glossophaga*.

The extralimital record of *G. s. antillarum* from the Bahamas is certainly not accurate (see Baker and Genoways, 1978; Koopman *et al.*, 1957), but it is difficult to explain how this record originated. Dr. J. Percy Moore collected mammals in the Bahamas in November 1890, and Rehn (1902b) described *Nyctinomus bahamensis* (= *Tadarida brasiliensis bahamensis*) from his collection. Moore then continued to Jamaica in December 1890 and took several bats there, one of which became the holotype of *G. s. antillarum*. It is possible that a specimen of *Glossophaga* was inadvertently placed in a jar containing specimens from the Bahamas. Buden (1986)

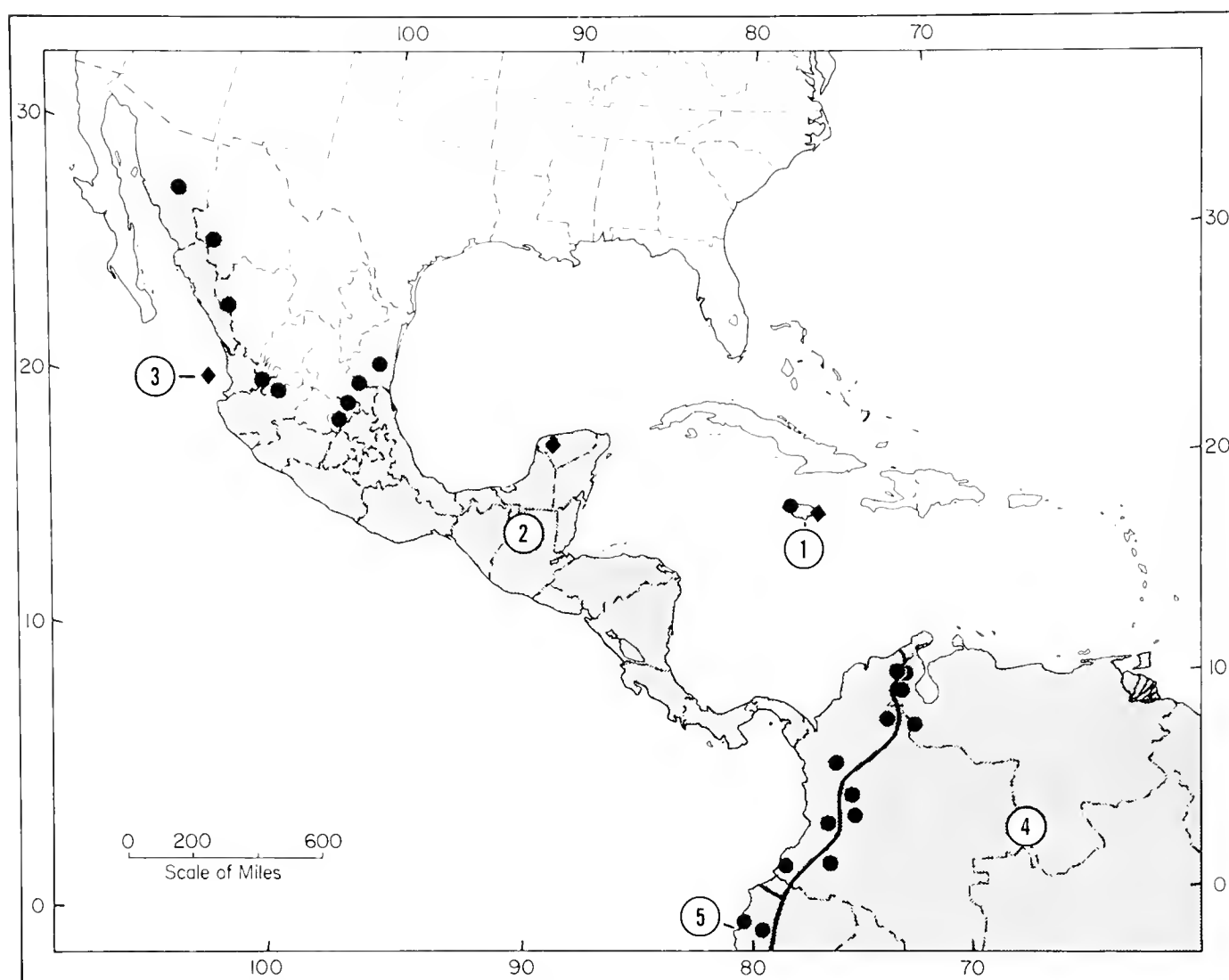


FIG. 27.—Geographic distribution of *Glossophaga soricina* in North America and northern South America. Recognized subspecies are *G. s. antillarum* (1), *G. s. handleyi* (2), *G. s. mutica* (3), *G. s. soricina* (4), and *G. s. valens* (5). Circles represent marginal localities and diamonds represent type localities.

considered the Bahamian record to be an “accidental,” inasmuch as he never collected *G. soricina* in 20 years of field investigations on the islands, nor have fossils been found in the extensive material recovered from the Bahamas (Morgan, 1989). Rehn (1902a) mentioned this specimen from the Bahamas, and G. M. Allen (1911) somewhat cryptically suggested that it came from New Providence. I have examined the specimen in question (ANSP 5098), and the specimen label simply reads “Bahamas.”

Evidently, *G. s. antillarum* prefers to roost in small, relatively dry caves, sometimes in association with *Macrotus waterhousii* and *Artibeus jamaicensis* (Goodwin, 1970). Pregnant females have been collected in January, and lactating females have been taken in May and July. There may be sexual segregation during part of the year in that males and females were found roosting separately during December and January (Goodwin, 1970).

Selected external measurements of two male and three female *G. s. antillarum*, respectively, are: total length, 68, 65, 61, 68, 63; length of tail, 5, 7, 9, 8, 6; length of hind foot, 12, 12, 12, 12, 12; and length of ear from notch, 15, 15, 14, 14, 13.

Specimens examined (24).—JAMAICA. *Clarendon*: Portland Cave, 1 mi. W Mahoe Gardens, 4 (USNM); Portland Point, 2 (AMNH); Portland Ridge, 1 (AMNH). *St. Ann*: Green Grotto, 2 mi. E Discovery Bay, 1 (TTU); Hounslow, Money Cave, 1 (AMNH); Mason River Research Station, 2.5 mi. W Kellits, 1 (TTU); Mosely Hall, Mosely Hall Cave, 1 (AMNH); 4 mi. E Runaway Bay, 3 (TTU); 0.5 mi. S, 0.5 mi. W Runaway Bay, 1 (TTU). *St. Catherine*: Yallahs, 4 (TTU). *St. James*: Montego Bay, Sewell Cave, 1 (AMNH). *St. Thomas*: Port Antonio, 3 (1 AMNH, 2 USNM). *Trelawny*: N & W Quick Step, 1 (USNM).

Additional records.—JAMAICA. *St. Ann*: Orange Valley (Baker and Bass, 1979). *St. Catherine*: Riverhead Cave (Henson and Novick, 1966); River Sink Cave (McNab, 1976). *St. James*: Sewell (Goodwin, 1970). *St. Mary*: 4 mi. E Oracabessa (Goodwin, 1970).

Marginal records.—JAMAICA.

Glossophaga soricina handleyi Webster and Jones

1980. *Glossophaga soricina handleyi* Webster and Jones, *Occas. Papers Mus.*, Texas Tech Univ., 71:5, 7 November.

Holotype.—Adult male, skin and skull, TTU 25893, from the grounds of Colegio Peninsular, Mérida, Yucatán, México; obtained on 1 April 1975 by J. B. Bowles, original no. 2262. Holotype examined; zygoma damaged, but skin and skull otherwise in excellent condition.

Measurements of the holotype.—Total length, 63; length of tail, 8; length of hind foot, 11; length of ear from notch, 14; length of forearm (dry), 34.4; greatest length of skull, 21.0; condylobasal length, 19.5; zygomatic breadth, 9.3; mastoid breadth, 8.9; interorbital breadth, 4.1; length of maxillary toothrow, 7.2; length of mandibular toothrow (c-m3), 7.6; weight, 9.0 grams.

Distribution.—Known from northern México (Sonora in the west and Tamaulipas in the east) southeastward throughout Middle America to northern and western Colombia (Fig. 27); known altitudinal distribution from sea level to approximately 2600 meters in elevation.

Comparisons.—A medium-sized race of *G. soricina*, both externally and cranially (Table 16). The postorbital swellings are greatly inflated in *G. s. handleyi*, the zygoma converge anteriorly, the pterygoid alae are well developed, the large lower incisors usually are in contact, and the rostral slope is moderate relative to that of other races. The pelage averages paler than that in *G. s. soricina*, but darker than that in *G. s. antillarum*, *G. s. mutica*, and *G. s. valens*. The subspecies *handleyi* appears to be, at least in terms of overall morphology and size, intermediate between *G. s. soricina* and the isolated races from the Tres Mariás Islands, Jamaica, and western South America.

Reproduction.—Data on reproductive condition were available from 361 female *G. s. handleyi* (Table 19). Pregnant females have been collected in all months ex-

TABLE 19.—*Recorded reproductive activity in females of Glossophaga soricina handleyi.*

Month	Number examined	Number pregnant	Number lactating
January	36	15	0
February	41	27	1
March	54	17	6
April	49	10	9
May	28	6	9
June	38	3	4
July	35	4	10
August	20	3	3
September	22	10	1
October	4	0	0
November	12	1	1
December	22	0	3

cept October and December, but, as represented in collections, were more common from January to March and September. Lactating females have been taken in all months except January and October, but more females were in nursing condition in May and July. Average length of testes, followed by sample size in parentheses, for males collected in the months from January through August was 2.7 (3), 3.4 (5), 3.7 (3), 3.5 (2), 3.8 (4), 3.8 (5), 4.0 (2), and 2.8 (4). Thus, it appears that the reproductive strategy of *G. s. handleyi* is that of monotocous bimodal polyestry at any given locality (Fleming *et al.*, 1972; Wilson, 1973). However, reproductively active females have been taken in all months of the year over the geographic range of the subspecies.

Remarks.—*G. s. handleyi* is one of the most commonly encountered bats in México and Central America, and, consequently, some aspects of its ecology and natural history are relatively well known. Nonetheless, there appear to be few differences in the biology of *G. s. handleyi* and that of *G. s. soricina* of South America. Therefore, it is discussed in the species account of *G. soricina*.

Average external measurements (extremes in parentheses) of 147 males, followed by those of 151 females, of *G. s. handleyi* are: total length, 63.0 (51-73), 64.7 (52-79); length of tail, 7.9 (4-13), 8.0 (4-12); length of hind foot, 10.6 (6-13), 10.9 (9-17); length of ear from notch, 13.8 (9-16), 14.2 (8-16). Seventy-seven males and 57 nonparous females averaged 9.8 (7.0-15.0) and 10.2 (8.3-13.4) grams in weight, respectively.

Specimens examined (2923).—BELIZE. *Belize*: Ladyville, 2 (TTU); Rockstone Pond, 16 (ROM). *Cayo*: Augustine, 38 (35 ROM, 3 TTU); Toledo Colombia Forest, Cirque Negro, Collins Trail, 1 (USNM). *Corozal*: Chan-Chen, 1 (FMNH); 0.75 mi. E Corozal, 2 (LSU). *Stann Creek*: Canada Hill, 10 mi. W Stann Creek, 1 (TCWC). *Toledo*: Maya Mountains, 1 (TTU); Ontario, 3 (TTU); Puebla Viejo, 1 (FMNH); San Antonio, 1 (FMNH). *No locality*: 11 (MSU). COLOMBIA. *Antioquia*: San Jeronimo, 720 m., 1 (FMNH); Urabá, Río Currales, 50 m., 1 (FMNH). *Bolívar*: Cartagena, Barrio Boca Grande, 1-2 m., 2 (FMNH). *Cordoba*: Jaraquiel, 1 (CMNH). *Guajira*:

Villanueva, 2 (USNM). *Magdalena*: Aguachica, 1 (CMNH); Bonda, 6 (AMNH); Cuchilla de (Las) Marimonda, 1 (USNM); Santa Marta, Mamatoco, 1 (CMNH). *Nariño*: 80 mi. from Buenaventura (Ecuador), sea level, 1 (AMNH). *Valle del Cauca*: Atuncela, 1 (USNM); Buenaventura, 3 (USNM); Hormiguero (Hormigulro), ca. 20 km. SE Cali, 1000 m., 2 (USNM); 2 km. SE Jamundí, 1 (USNM); La Habana, 20 km. E Buga, 1 (USNM); Pueblo "El Tambor," ca. 15 km. NW Vijes, 1 (USNM); Río Cauca, Ríofrio, 3500 ft., 5 (AMNH); Río Zabaletas, 29 km. SE Buenaventura, 1 (USNM). *COSTA RICA*. *Alajuela*: Grecia, 33 (AMNH); Santa Clara, 600-700 ft., 2 (LSU). *Cartago*: Agua Caliente, 1 mi. S Cartago, 26 (UMMZ); Santa Teresa Peralta, 3 (AMNH); Tres Rios, 6 (AMNH); Instituto Interamericano, 3 mi. E Turrialba, 602 m., 1 (UMMZ); La Dominica, 1 mi. N Turrialba, 10 (USNM); 0-0.5 mi. SW Turrialba, 600-620 m., 2 (1 LSU, 1 UMMZ); 0.5-1 mi. W Turrialba, 620-700 m., 5 (UMMZ). *Cortes*: Finca Fe, 1 mi. NW Jaral, 2300 ft., 1 (LSU). *Guanacaste*: 9 mi. S Las Cañas, 35 m., 10 (UMMZ). *Limón*: Finca La Lola, 50 m., 6 (LSU). *Puntarenas*: Boca de Río Barranca, 3 (UMMZ); Dominical, 1 (UMMZ); 10 mi. SE Palmar Sur, 1 (LSU); Rincón de Osa, sea level, 3 (LSU); San Francisco Esparata, 17 (AMNH); San Vito de Java, 1200 m., 1 (UMMZ); Tambor, Nicoya, 1 (UMMZ). *San José*: Alto Escazu (Escaza), 3000 ft., 17 (AMNH); Fuentes, 10 (1 AMNH, 5 FMNH, 4 USNM); La Uruca, 53 (AMNH); Pevas (Las Paras), 4 (AMNH); Santa Ana, 10 (LSU); 0-2 mi. NW San José, ca. 1135 m., 15 (8 AMNH, 3 KU, 2 UMMZ, 2 USNM); San Pedro (Montes de Oca), 5 (4 FMNH, 1 LSU); Virill and Barreal Caves, San Jose, 25 (UMMZ). *No locality*: 5 (AMNH). *EL SALVADOR*. *Chalatenango*: 20 km. W Chalatenango, 250 m., 8 (TCWC). *Cuscatlán*: 2 km. W Suchitoto, 380 m., 4 (TCWC); 14 km. NW Suchitoto, 250 m., 2 (TCWC). *La Libertad*: Los Chorres, 3.5 km. N, 6.5 km. W Nueva San Salvador, 2300 ft., 1 (TCWC); 3.5-20 km. W La Libertad, 15-250 m., 5 (TCWC). *San Salvador*: San Salvador, 680 m., 1 (KU); 6 mi. E San Salvador, 1 (KU). *Santa Ana*: Lake Coatepeque, 1 (AMNH). *Sonsonate*: 31 km. W La Libertad, sea level, 3 (TCWC). *GUATAMALA*. *Alta Verapaz*: 1 mi. W Languín, 2000 ft., 1 (TCWC); no locality, 2 (AMNH). *Baja Verapaz*: 2 km. SE Salamá, 950 m., 2 (TCWC); San Miguel Chicáj, 950 m., 1 (TCWC). *Chiquimula*: 20 km. SSE Chiquimula, 550 m., 2 (TCWC); Jocotán, near Chiquimula, 1350 ft., 2 (KU). *El Petén*: Chuntuqui River, 1 (USNM); 2 mi. S Flores, 1 (AMNH); La Libertad, 20 (AMNH); Uaxactún, 1 (UMMZ). *El Progreso*: El Progreso, 3 (AMNH); ca. San Antonio La Paz, km. 35, 3200 ft., 2 (TCWC). *Escuintla*: El Zapote, 2 (FMNH); Hda. El Rosario, 950 m., 6 (UMMZ); 2 mi. E Palín, 4000 ft., 1 (TCWC). *Guatemala*: Amatitlán, 3800 ft., 2 (TCWC); Lake Amatitlán, 4000 ft., 1 (KU). *Huehuetenango*: Barillas, 1 (AMNH). *Izabal*: Las Iscobas, 1 (FMNH); Puebla, 1 (AMNH); 22-25 km. SSW Puerto Barrios, 200-300 ft., 10 (TCWC). *Jutiapa*: 7 mi. S Ascunción Mita, 4 (FMNH); Finca El Carnero, 4 (2 FMNH, 2 UMMZ); Jutiapa, 7 (FMNH); 15 km. NE Jutiapa, 3000 ft., 2 (TCWC). *Quiché*: 1 km. WNW Sacapulas, 1200 m., 1 (TCWC). *Retahuleu*: 3 km. N Retahuleu, 1000 ft., 1 (TCWC). *San Marcos*: El Porvenir, 13 (5 FMNH, 8 UMMZ); Finca Carolina, 2 (AMNH); Hda. California, 2 (AMNH). *Santa Rosa*: Astillero, 25 ft., 1 (KU); Chiquimulilla, 7 (USNM); 3 km. S, 6 km. E Cuilapa, 2400 ft., 1 (TCWC); Finca El Progreso, 2 (UMMZ); Finca El Zapote, 1 (UMMZ); ca. La Avellana, 13 (6 AMNH, 7 USNM); Monterico, 2 (AMNH). *Sololá*: San Lucas, 3 (AMNH). *Suchitepéquez*: El Ciprés, 5 (AMNH); *Zacapa*: El Rancho, 1 (FMNH). *HONDURAS*. *Atlántida*: 7 mi. E La Ceiba, 100 ft., 1 (TCWC); 17 mi. W La Ceiba, 50 ft., 2 (TCWC); Lancitilla, 25 ft., 5 (1 KU, 4 TCWC); 4 mi. S Tela, 25 ft., 2 (TCWC). *Choluteca*: 36 km. SE Choluteca, 600 m., 14 (TCWC). *Comayagua*: Comayagua, 580 m., 2 (TCWC); 17 km. S Comayagua, 580 m., 1 (TCWC). *Copán*: Copán, 660 m., 13 (TCWC); Ruinas de Copán, 12 (TCWC); 5 km. E Santa Rita, 750 m., 1 (TCWC). *Cortés*: El Olivo, 1 (CMNH); La Lima, 40 m., 4 (TCWC); 2 mi. W San Pedro Sula, 100 ft., 4 (TCW). *El Paraíso*: 6-21 km. E Danlí, 460-680 m., 4 (TCWC); 1 km. SE Danlí, 780 m., 1 (TCWC); 7 mi. N Güinope, 15 (TCWC); 7 mi. S Zamorano, 2800 ft., 3 (TCWC). *Francisco Morazán*: Comayagüela (Comayabuela), 9 (2 AMNH, 7 CMNH); Escuela Agrícola Panamericana, 2 (TCWC); La Flor Archaga, 18 (AMNH); San Marcos Mine, 2

mi. SE Sabana Grande, 1500 ft., 4 (TCWC); 10 mi. NE Talanga, 3400 ft., 1 (TCWC); 12 mi. N Tegucigalpa, 2800 ft., 23 (TCWC); 0-6 mi. N El Zamoranao, 2800 ft., 8 (TCWC). *Gracias a Dios*: Brus Laguna, 10 ft., 2 (TCWC); Las Flores, 1 (AMNH). *Intibucá*: La Esperanza, 1660 m., 2 (TCWC). *Islas de las Bahía*: Isla de Roatán, Coxen Hole, 2 (FMNH); Isla de Roatán, Roatán, 11 (TCWC); Isla de Roatán, 1 (ROM); Isla de Utila, cave NE end, 2 (ROM); Isla de Utila, 2 mi. N Utila, 4 (TCWC). *La Paz*: Cueva del Viejo, 2 mi. W La Paz, 1800 ft., 7 (5 CMNH, 2 TCWC). *Ocotepeque*: 1 km. N (Nueva) Ocotepeque, ca. 1000 ft., 7 (TCWC); 1 km. W Nueva Ocotepeque, 840 m., 6 (TCWC); 1 km. NW Nueva Ocotepeque, 840 m., 2 (TCWC). *Olancho*: 12.1 mi. (by road) SSW Dulce Nombre de Culmi, 3 (TTU); Juticalpa, 1200 ft., 6 (TCWC). *San Marcos*: Sabana Grande, 26 (AMNH). *Santa Bárbara*: 0-5 km. NE La Llama, 120 m., 4 (TCWC); 0-7 km. N Santa Barbara, 120 m., 8 (6 AMNH, 2 TCWC). *Valle*: 6 km. E Amatilla, 60 m., 1 (TCWC); 10 mi. SSW Nacaome, 1 (TTU). *Yoro*: 0-8 km. W Yoro, 680-720 m., 5 (TCWC). **MEXICO. Campeche**: Apazote, near Yohalluñ, 5 (USNM); 49 km. S Campeche, San José Carpizo, 14 (UMMZ); 10 km. SSW Champotón, 10 m., 37 (KU); 103 km. SE Escárcega, 2 (KU); Isla de Carmen, Ciudad del Carmen, 9 (KU); San José Carpizo, 12 (FMNH). **Chiapas**: 5-8 km. N Arriaga, 600-2500 ft., 10 (TCWC); Cueva Llano Ridondo, 3 km. N Las Margaritas, 1500 m., 2 (KU); 3 km. W Cuipa, 1600 ft., 4 (TCWC); 2 km. S El Paraiso, 3100 ft., 4 (KU); 13 mi. S Las Cruces, 48 (KU); 15 mi. SW Las Cruces, 9 (KU); 17 mi. W, 4 mi. S Las Cruces, 91 (KU); Las Margaritas, 1500 m., 1 (KU); 13-18 mi. S La Trinitaria, 2800 ft., 11 (10 KU, 1 TCWC); Los Amates, 6 (TCWC); 6 km. NE Mal Paso, 400 ft., 1 (TCWC); Mapastepec, 45-65 m., 6 (UMMZ); 16 mi. NW Palenque, 100 ft., 3 (TCWC); 4 km. NE Pichucalco, 100 m., 23 (KU); 8 mi. ENE Pichucalco, 200 ft., 1 (MSU); 4-5 km. ESE Pichucalco, 100 m., 7 (TCWC); Ruinas de Palenque, 300 m., 8 (KU); Sabana San Quintín, 6 (KU); 4 km. ENE San Lucas (Cueva Leon), 1 (TCWC); 2 km. NW San Lucas, 2 (TCWC); 3 mi. SSE Soyaló, 3000 ft., 3 (TCWC); 4 km. NW Tapachula, 450 ft., 4 (TCWC); 3.8 mi. SW Tapachula, 2 (TTU); 15 km. SE Tonalá, 100 ft., 3 (TCWC); 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa, 18 (TTU); 8 mi. S Tonalá, Finca Ocuilapa, 1 (MSB); 1-3 mi. SE Tuxtla Gutiérrez, ca. 2600 ft., 93 (34 AMNH, 37 KU, 22 TCWC); 35-40 mi. SSE Tuxtla Gutiérrez, 1800-2200 ft., 25 (TCWC); 1 mi. S Tuxtla Gutiérrez, 20 (5 TTU, 15 UMMZ); 2 mi. SE Tuxtla Gutiérrez (Municipal Park), 7 (TCWC); Villa Flores, 600 m., 5 (UMMZ); 1.3 mi. SE Zapaluta (Cueva de Zapaluta), 5700 ft., 5 (TCWC); ca. 11-14 mi. SSE Zapaluta, 2700-3200 ft., 13 (TCWC). **Chihuahua**: La Bufa, 3500 ft., 1 (KU); 1.5 mi. SE Tocuina (Tacuina), 1500 ft., 1 (KU). **Colima**: 1 mi. N Coquimatlán (Coquinitlán), 1 (MSB); 2 km. SE Hda. Los Ortices, 1 (UMMZ); 23 mi. SE Manzanillo (Rt. 80), 1 (UMMZ); ca. 1 km. SE Jct. Manzanillo-Cuyutlán Hwy., 4 (LSU); 3 km. SE Ortices, 100 ft., 3 (OU); Pueblo Juárez, 2 mi. S Colima, 1 (AMNH); 1 km. W San Antonio, 2 (OU); 3 km. S Santiago, 1 (KU); 4 km. W Santiago, 2 (KU); 11 mi. NW Santiago, 100 ft., 2 (MSU); Terro Tepic, Valle de Brauderas, 2 (AMNH). **Distrito Federal**: Chicomostoc, Cerro Teutli, 2.8 mi. NNW Milpa Alta, 2620 m., 9 (8 KU, 1 UNAM). **Durango**: Chacala, 5 (USNM); Pueblo Nuevo, 1 (MSU); Santa Ana, 12 mi. SE Cosalá (Sinaloa), 1300 ft., 4 (KU). **Guerrero**: 2 mi. NW Alcapulco, 50 ft., 2 (KU); 5 km. N Colotlipa, Grutas de Juxtlahuaca, 800 m., 8 (KU); 4.5 mi. NE Cuajinicuilapa, 300 ft., 1 (MSU); El Carrizal, 1.9 km. W Hwy. 200, 8 (TTU); 13 km. N Iguala, km. 184, 3 (UMMZ); 3 mi. N El Ocotito, 4 (UMMZ); 38.5 km. N Río La Unión, 15 (TTU); 1 mi. SE San Andrés de la Cruz, 700 m., 4 (UMMZ); 8 mi. (by road) NE San Jerónimo, 25 m., 4 (UMMZ); 6 km. SSW Teloloapan, 1740 m., 2 (KU); 4 km. NW Teloloapan, Alpíaxia, 1540 m., 3 (KU); 8 mi. N, 1 mi. W Teloloapan, 3600 ft., 2 (KU). **Hidalgo**: El Suspiro, 1 km. N, 4 km. W Tehuetlán, 2 (TTU); 4 km. E San Felipe Orizatlán, ca. 500 m., 7 (TTU); 8 km. S Tlanchinol, 1 (TTU). **Jalisco**: Cerro Ameca, 5 mi. NNW Ameca, 5500 ft., 4 (KU); Estación Chamela, 6 km. E Chamela, 50 ft., 2 (MSU); Etzatlán (Itzatlán), 3500 ft., 1 (USNM); 2 mi. ENE Magdalena, 5000+ ft., 4 (KU); 12 mi. NE Pihuamo, 3150 ft., 2 (MSU); Puerto Vallarta, 25 ft., 1 (MSU); 4 mi. NNE Teuchitlán, 6 (5 KU, 1 MSU); 2 mi. NE Tomatlán, 8 (TTU). **México**: 4 mi. WSW Valle de Bravo, 5900 ft., 2 (MSU). **Michoacán**: 0.5 mi. E Coalcomán,

7 (UMMZ); 0.25 mi. SE Estopilas de Salitre, 1 (UMMZ); 12 mi. S Tzitzio (Huetamo Rd.), 1050 m., 1 (UMMZ). *Morelos*: Cuernavaca, 2 (USNM). *Nayarit*: 0.4 km. W Acaponeta, Hwy. 15, 6 (TTU); 8 mi. S Ahuacatlán (by road), 5 (USNM); Arroyo de Juguite, Río Santiago, 9 (USNM); 4 km. S Aticama, 1 (USNM); Chacala, 13 (USNM); 10 mi. N Compastela, 8 (MSU); 9 mi. WNW Compastela, 3 (MSU); 1 mi. S Cuautla, 1 (USNM); Cucharras, Río Acaponeta, 10 (USNM); El Refilión, 4 (USNM); 2 mi. E Jalcocotán, 18 (USNM); 2 mi. SE Jalcocotán, 3000 ft., 1 (MSU); 1 mi. NE Las Piedras, Río Tigrera, 2 (USNM); 6 mi. SSE Las Varas, 2 (MSU); 1 mi. S Lo de Marcos, 1 (USNM); Mineral del Tigre, 6 mi. E Huajicori, 1340 ft., 7 (MSU); Paso de Soquipa, 8.8 mi. E San Blas, 8 (USNM); Rancho Palo Amarillo, 7 (AMNH); Río Cañas, *ca.* La Concha (Sinaloa), state line, 1 (USNM); 0-3 mi. E San Blas, 75 ft., 20 (6 MSB, 2 UMMZ, 12 USNM); 4 mi. S, 5 mi. E San Blas, 44 (MSB); 2 mi. SE San Juan de Abajo, 3 (USNM); 0.5 mi. N, 0.7 mi. E Santa María del Oro, 3 (TTU); 1.4 mi. N Tacote, 8 (USNM); Teponahuastla, 2 (USNM); 17 mi. SE Tuxpan, 480 ft., 3 (MSU). *Oaxaca*: Chicapa, *ca.* 40 m., 3 (2 KU, 1 USNM); 0.5 mi. W Chiltepec, 5 (AMNH); El Guamól, km. 889, 9.5 mi. W Zanatepec, 2 (USNM); 13 mi. ENE Juchitan, 4 mi. E Jct. 185 on Rt. 190, 2 (UMMZ); 20 mi. NE La Ventosa, 8 (AMNH); 6-24 mi. N Matias Romero, 77 (66 AMNH, 4 TTU, 7 USNM); 17 mi. N, 2 mi. E Matias Romero, 2 (USNM); 1.7-9.5 mi. S Matias Romero, 13 (8 USNM, 5 TTU); 3 mi. W Milta, 2 (KU); Pinotepa (Nacional), 75-700 ft., 13 (7 AMNH, 6 USNM); 10 mi. N Puerto Escondido, 2050 ft., 1 (MSU); 4 mi. S Putla, 2750 ft., 2 (MSU); 5 mi. ESE Rio Grande, 100 ft., 1 (MSU); Río Guamól, Hwy. 190, 34 mi. S La Ventosa Jct., 1 (MSB); San Bartolo, 1 (AMNH); San Carolos, 1 (AMNH); 2 mi. E San Gabriel Mixtepec, 1 (AMNH); 0.5 mi. SE San Gabriel Mixtepec, 1 (AMNH); San Gerónimo, 4 (FMNH); Santa Efigenia, 550-1500 ft., 3 (USNM); Santa Maria Chimalapa, 3 (AMNH); 1 mi. S Sarabia, 1 (AMNH); *ca.* 10 mi. Tapanatepec, *ca.* 300 ft., 28 (22 AMNH, 4 KU, 2 TTU); 2 mi. S Tolosita (Tollocito), 2 (KU); 2 mi. SE Totolapan, 1 (MSU); Tuxtepec, 300 ft., 1 (USNM); 31.2 mi. SE Tuxtepec, 1 (TTU); Vista Hermosa, 1 (KU); Zacatepec, Mazatlán, 1 (AMNH); Zacatepec, 18 mi. NW Sola la Vega, 5 (AMNH). *Puebla*: 2 km. NW Alazán, 20 m., 2 (TCWC); 1 mi. E Raboso, 4350 ft., 5 (KU); Tuchitan, 1 (USNM); 2 mi. W Villa Avila Camacho, 250 m., 3 (TCWC). *Querétaro*: Hda. X-Conca, 2 mi. SSE Conca, 2 (TCWC); 3.7 mi. NW Jalpan, 2500 ft., 1 (TCWC); 8.2 mi. S Peña Blanca, 1 (TCWC). *Quintana Roo*: Felipe Carrillo Puerto, 30 m., 3 (KU); Isla de Cozumel, 4 (KU); 8 km. N, 5.5 km. E Playa del Carmen, 1 (TTU); Rancho de Pirata, Isla Mujeres, 1 (KU). *San Luis Potosí*: Ebano, 4 mi. SSW Ajinche to Oviedo, 1 (LSU); El Salto Falls (Salto del Agua), 11 (10 AMNH, 1 USNM); 7-10 km. N Tamazunchale, 10 (LSU); 10 km. N Tepeyac, 1 (TTU); 20 km. N Valles, 5 (LSU); 8 km. NE Valles, Cueva de Los Sabinas, 5 (TTU); 25 km. W Valles, 1 (TTU); *ca.* Xilitla, 13 (2 AMNH, 11 LSU); 9 mi. NNE Xilitla, 6 (LSU); 3.5 mi. NW Xilitla, 2200 ft., 2 (TCWC). *Sinaloa*: 0.5 mi. N Comitán, 1 (MSB); 1.9 mi. NE Concordia, 7 (TTU); Escuinapa, 100 ft., 23 (22 AMNH, 1 TCWC); Isla Palmito del Verde, 4 (KU); 1 mi. E Malpica, 300 ft., 3 (MSU); 3.2 mi. N Rosario, 15 (TTU); 0.5 mi. W Rosario, 100 ft., 1 (MSU); 0-2.5 mi. E Santa Lucía, 3200-3600 ft., 8 (KU). *Sonora*: 0-0.5 mi. N Aduana, 18 (MSB); 0.25 mi. W Aduana, 1600 ft., 3 (1 KU, 2 MSB); 4 mi. N Alamos, 3 (KU); 0.5-10 mi. E Alamos, 3 (MSB); 6 mi. W Alamos, 2 (MSB); Bahia San Carlos, 1 (AMNH); 28 mi. E Mazatán, 1 (MSB); Minas Nuevas, 4 mi. NW Alamos, 7 (TTU); Río Cuchijaqui, 1 (TTU); Río Mayo, San Bernardo, 1 (UMMZ); Vado Cuchijaqui, 9 mi. ESE Alamos, 2 (KU); 5.5 mi. W Tónichi, 1 (TTU); no locality, 1 (USNM). *Tabasco*: Balancán, 2 (LSU); Montecristo, 5 (USNM); 18 mi. N, 1.5 mi. E Teapa, 1 (LSU); 1-2.75 mi. E Teapa, 47 (45 LSU, 2 UMMZ); 5 mi. SW Teapa, 10 (KU); 13.6 mi. W Villahermosa, 2 (TTU); 26.9 mi. W, 1.8 mi. S Villahermosa, Hwy. 180, 5 (TTU). *Tamaulipas*: Altamira, 2 (USNM); 8 km. NE Antigua Morelos, 500 ft., 1 (KU); 5 mi. NW Antigua Morelos, El Pachón Cave, 18 (AMNH); (Ejido) Ojo de Agua, 20 mi. N El Mante, Río Sabinas, *ca.* 300 m., 2 (KU); El Encino, Río Sabinas, 2 (USNM); 30 mi. NNW El Mante, 300 m., 1 (TCWC); La Gruta de Quintaro, km. 545 S El Mante, 7 (TTU); Sierra de Tamaulipas, 16 mi. W, 3 mi. S Piedra, 1400 ft., 2 (KU); 67 km. S Ciudad Victoria, Hwy. 85, 1

(TTU); no locality, 400 ft., 1 (KU). *Veracruz*: Achotal, 7 (FMNH); 3 km. W Acultzingo, 7000 ft., 1 (KU); Boca del Río, 10 ft., 4 (KU); 0-5 mi. S Catemaco, 1000 ft., 7 (2 KU, 5 USNM); 4 km. WNW Fortín, 3200 ft., 4 (KU); 3 km. W Gutiérrez Zamora, 300 ft., 1 (KU); Jalapa, 2 (USNM); 35 km. ENE Jesús Carranza, 150 ft., 1 (KU); Mirador, 1 (USNM); 3 mi. NW Nautla, 1 (KU); Ojo de Agua, Río de Atoyac, 3 (2 CMNH, 1 TTU); 10 km. NW Papantla, 750 ft., 1 (KU); 4 km. W Paso de San Juan, 5 (KU); 0-8 km. NW Potrero del Llano, 350-1700 ft., 4 (KU); Potrero Viejo, 7 km. W Potrero, 10 (KU); 3 km. E San Andrés Tuxtla, 1000 ft., 2 (KU); 2 mi. W San Andrés Tuxtla, 1 (AMNH); San Marcos, 200 ft., 3 (KU); 4 km. W, 5 km. S Sontecomapan, 1 (TTU); 4.1 km. S, 2.3 km. W Tenochitlán (Tenochitlán), 1 (UMMZ); 12.5 mi. N Tihuatlán, 300 ft., 6 (KU); 82 km. N (by road) Tuxpan, 3 (TTU); 0-35 km. NW Tuxpan, *ca.* 1000 ft., 16 (KU); 76 km. NW (by road) Tuxpan, Rancho Piedra Clavades, 2 (TTU); 0-24 mi. S Veracruz, 24 (17 AMNH, 7 USNM); no locality, 6 (FMNH). *Yucatán*: Calcehtok, 55 mi. S Mérida, 6 (1 AMNH, 5 UMMZ); Chichén Iztá, 1 (AMNH); Cueva de Spukil, 3 km. S, 1 km. W Calcehtok, 2 (TTU); El Laberinto, 1 (AMNH); Gruta de Balankanche, 5 km. W Chichén Iztá, 6 (KU); 0-4 mi. S Mérida, 5 (2 KU, 3 TTU); 55 km. SSW Oxkintok, 5 (UMMZ); 13 km. W Peto, 13 (KU); Pisté, 10 m., 2 (KU); Santa Rosa, 20 km. S Peto, 2 (UMMZ). *Zacatecas*: 5.5 mi. S Moyahua, 4000 ft., 1 (KU); 1 mi. N Santa Rosa, 3700 ft., 1 (MSU). *Nicaragua*. *Boaco*: Los Cocos, 14 km. S Boaco, 3 (KU); Santa Rosa, 17 km. N, 15 km. E Boaco, 300 m., 2 (KU); 4 km. W Teustepe, 140 m., 3 (KU). *Carazo*: 3 mi. NNW Diriamba, 1 (KU); 3 km. N, 4 km. W Diriamba, 7 (KU); La Trinidad, 1 (AMNH). *Chinandega*: 4.5 km. N Cosigüina, 15 m., 7 (KU); Hda. Bellavista, Volcán Casita, 720 m., 8 (KU); Hda. San Isidro, El Realejo, 10 km. S Chinandega, 10 m., 5 (2 AMNH, 3 KU); San Antonio, 15 m., 9 (KU); Volcán de Chinandega, 1 (AMNH). *Chontales*: Hda. Bellavista, Volcan Casita, 720 m., 8 (KU); Hato Grande, 13 km. S, 8 km. W Juigalpa, 60 m., 1 (KU). *Estalí*: Condega, 540 m., 5 (KU); 5 km. N, 9 km. E Condega, 800 m., 1 (KU); 2 mi. S Estalí, 3300 ft., 2 (TCWC). *Granada*: Finca Santa Cecilia, 6.5 km. SE Guanacaste, 660 m., 4 (KU). *Isla de Omotepe*: 0.5 km. W Alta Gracia, 110 m., 1 (KU); Merida, 40 m., 1 (KU); Moyogalpa, 40 m., 14 (KU); 4.5 km. W San José del Sur, 1 (KU). *León*: 1 mi. ENE Poneloya, 1 (KU). *Madriz*: San Juan del Río Coco (Telpaneca), 3 (AMNH); Yalagüina, 10 km. E Somoto, 2200-2300 ft., 4 (TCWC). *Managua*: El Boquerón, 4 (KU); 6 km. N El Tuma, 550 m., 7 (TCWC); Las Jinotepe, 8 km. SW Managua, 1 (KU); 0-3 km. N Sabana Grande, *ca.* 50 m., 6 (KU); 3 km. N, 0.5 km. E Sabana Grande, 1 (KU). *Matagalpa*: 2 mi. SE Dario, 1500 ft., 7 (TCWC); 2 km. N, 6 km. E Esquipulas, 960 m., 1 (KU); 1 km. NE Esquipulas, 420 m., 3 (KU); Finca Tepeyac, 10.5 km. [sic], 9 km. E Matagalpa, 960 m., 5 (KU); Hda. La Cumplida, 19 km. N Matagalpa, 1 (UMMZ); La Danta, 1 km. N, 5 km. E Esquipulas, 780 m., 2 (KU); 4 mi. E Matagalpa, 2600 ft., 7 (TCWC). *Nueva Segovia*: 1.5 km. N, 1 km. E Jalapa, 660 m., 2 (KU); Quilali (Juilali), 1 (AMNH). *Rivas*: Finca Amayo, 13 km. S, 14 km. E Rivas, 40 m., 20 (KU); 11 km. S, 3 km. E Rivas, 50 m., 9 (KU); 5.5-8 km. NE San Juan del Sur, 70-120 m., 9 (KU). *Zelaya*: 1 km. NW La Catiada, 1300 ft., 2 (TCWC); El Recreo, 25 m., 3 (KU); *ca.* 10 km. W Rama, 15-40 m., 10 (7 TCWC, 3 TTU). *Panama*. *Bocas del Toro*: Almirante, 11 (USNM); Boca del Drago, 1 (USNM); Changuinola, 4 (USNM); Isla Bastimentos, 2 (USNM); Isla Colón, 2 (USNM); Isla Escudo de Varaguas, 2 (USNM); Río Changena, 1 (USNM); Sibube, 1 (USNM). *Canal Zone*: Ancón, 8 (MSB); Balboa, 5 (FMNH); Barro Colorado Island, 7 (1 AMNH, 1 KU, 5 USNM); Bohío, 2 (USNM); Cerro Tigre, 1 (USNM); Coco Solo, 8 (USNM); Corozal, 6 (USNM); Empire Range, 15 (USNM); Fort Amador, 1 (MSB); Fort Clayton, 19 (USNM); Fort Davis, 6 (USNM); Fort Gulick, 1 (USNM); Fort Kobbe, 4 (USNM); Fort Randolph, 1 (USNM); Fort Sherman, 1 (USNM); Frijoles, 15 (USNM); Fuerte San Lorenzo, 3 (USNM); Isla Galeta, 3 (USNM); Gatún, 3 (UMMZ); Miraflores Locks, 7 (MSB); Paraiso, 13 (UMMZ); Quarry Heights, 1 (MSB); Río Mandinga, 3 (USNM); San Pablo, 10 (USNM). *Chiriquí*: Boquerón, 44 (36 AMNH, 8 FMNH); Cuestra de Piedra, 16 (USNM); David, 1 (USNM); El Volcán, 3 (USNM); Guabalá, 1 (USNM); La Gorgona, 1 (USNM); Pedregal, 3 (USNM); Progreso, 32 (USNM); San Vicente, 2 (USNM); Tolé, 5 (USNM); no locality, 3 (1

AMNH, 2 UMMZ). *Coclé*: Churubé at river, 11 (USNM); El Copé, 3 (USNM); Olá, 20 (USNM); Río Hato, 30 (USNM); Santa Clara, 16 (USNM). *Colón*: Portobelo, 1 (USNM). *Darién*: El Real, 5 (USNM); Jaqué, 9 (1 MSB, 8 USNM). *Los Santos*: Cerro Hoya, 4 (USNM); Las Palmitas, 26 (USNM); Los Santos, 3 (TTU). *Panamá*: Candelaria Hydrographic Station, 1 (USNM); Chilibrillo Caves, 1 (USNM); La Chorrera, 2 (1 AMNH, 1 USNM); Pacora, 3 (USNM); Panamá, 2 (UMMZ); Panamá Viejo, 2 (USNM). *Veraguas*: Isla Canal de Afuera, 3 (USNM); Isla Cébaco, 5 (USNM); Soná, 2 (USNM). *Province unknown*: Falleon, 1 (USNM).

Selected additional records.—COLOMBIA (Hershkovitz, 1949). *Magdalena*: Río Guaimaral; Sierra Negra, Sierra de Perijá. *Norte de Santander*: Guamalito. COSTA RICA. *Guanacaste*: Curiol de Santa Rosa, 25 m. (Starrett and Casebeer, 1969); Finca la Pacífica, 4 km. NW Cañas (Fleming *et al.*, 1972). *Province unknown*: Taboga (Howell and Burch, 1974). GUATAMALA. *Alta Verapaz*: Chipóc (Dickerman *et al.*, 1981; Goodwin, 1934); Finca Chicoyou, 1 km. W Cobán (Jones, 1966); Finca Los Alpes (Jones, 1966). *El Petén*: Tikal (McCarthy, 1982; Rick, 1968). MEXICO. *Campeche* (Jones *et al.*, 1973): Dzibalchén; 2 km. NE Hopelchén; La Tuxpeña. *Chiapas*: 42 km. W Cintalapa (Baker, 1967). *Chihuahua*: 40 km. N, 6 km. W Choix (Sinaloa), 2400 ft., (Anderson, 1972). *Colima* (Kennedy *et al.*, 1984): 0.5 mi. W Chiapa; 3 mi. E Cuyatlan; *ca.* El Cobano; 2 mi. E Estancia; 3.5 mi. ESE Estancia, *ca.* 1400 ft.; Playa de Oro (Torresillas); Torresillas. *Guerrero*: El Papayo, 25 ft. (Lukens and Davis, 1957); Río Xolapa, 14 km. SW Tierra Colorado, 600 ft. (Davis, 1944); 17 km. S Taxco, 4000 ft. (Lukens and Davis, 1957). *Jalisco* (Watkins *et al.*, 1972): 11 mi. SW Autlán, 710 m.; 10 mi. NNW Barro de Navidad; 2 mi. E Bolaños; 11-18 mi. W Chalapa, *ca.* 5000 ft.; 15 km. NW Cihuatlán; Cuitzamala, 25 ft.; 4 mi. N Durazno; 5 mi. S, 1 mi. E El Arado; 6 mi. E El Limón, 2700 ft.; El Salto, 24 mi. W Guadalajara, 4500 ft.; El Tabaco, 200 ft.; 2 km. NW Emiliano Zapata, 20 m.; 9-10 mi. N Guadalajara, 3350-4000 ft.; Ixtapa; Jilotlán de los Delores, 2400 ft.; 2 mi. N Milpillan, 3000 ft.; 2 mi. ESE Pan de Barrancas; *ca.* 20 km. Purificación, *ca.* 1400 ft.; 2 mi. S La Cuesta, 1500 ft.; 10 km. E Santiago (Colima); Sierra de Caule, 4100 ft.; Tolimán, 2200 ft. *Morelos*: Cañon del Lobo (Davis and Russell, 1954); Hda. San Gabriel (Davis and Russell, 1952); Puente de Ixtla (Davis and Russell, 1952). *Quintana Roo*: 500 [k]m. SSW Casa Principal de la Hacienda de Santa Rosa (Villa-R., 1967); Tulum (Tuloom) (Gaumer, 1917). *San Luis Potosí*: 2 km. SW Huichihuayán (Dalquest, 1953); Rancho Nacimiento del Río Coy, 16 mi. S Valles (Constantine, 1958). *Sinaloa* (Jones *et al.*, 1972, unless otherwise noted): 1.5 mi. N Badiraquato, 750 ft.; 11-16 mi. NNE Choix, *ca.* 1700 ft.; 0-1.5 km. W Copala, *ca.* 1400 ft.; 0-6 km. W Cosalá, 1300-1500 ft.; 0.5 mi. E El Cajón, 1800 ft.; 0-1 mi. S El Dorado; 6 km. E El Fuerte, 400 ft.; Matatán; *ca.* 5 mi. Mazatlán, *ca.* 10 ft.; 0-1 km. NE Pánuco, 2050-2700 ft.; 0-3 mi. SE Piaxtla (Camino Real), 100-500 ft.; 0-5 mi. WSW Plomosas, 800-2500 ft.; Río Piaxtla, Hwy. 15 (Baker, 1967); 6 km. SW San Blas, 30 ft.; San Ignacio, 700 ft.; San Juan; 0.5 mi. SE Vaca, 650 ft.; 8-12 km. N Villa Unión, 400-450 ft. *Sonora*: Chinobampo (Burt, 1938). *Tamaulipas* (Villa-R., 1967): Cueva de la Boca, 5 km. SW Cañon de la Boca, 22 [k]m. NNW Ciudad Victoria; Cueva de Quintero, 2 km. S Quintero, 250 m. *Yucatán* (Gaumer, 1917, unless otherwise noted): Actun Coyok, 3.5 km. SSE Oxkutzcab (Hatt *et al.*, 1953); Calotmul; Cenote de Chapultepec, Mérida (Villa-R., 1967); Chablé; Cuetzala (Hershkovitz, 1951); Izamal; Loltum, 5 km. SW Oxkutzcab (Hatt *et al.*, 1953); Motul; Tekom (Hershkovitz, 1951); Temax; Tzalam; Uxmal; Xbac; Yaxcach. PANAMA (Handley, 1966, unless otherwise noted). *Canal Zone*: Vijía (Vigía) (Goldman, 1920). *Chiriquí*: Bugaba (Goldman, 1920); Cerro Punta (Peterson and Kirmse, 1969). *Colón*: Colón. *Darién*: Cana (Goldman, 1920). *Los Santos*: Guanico. *Panamá*: Isla Saboga; Nueva Gorgona. *San Blas*: Mandinga.

Marginal records.—MEXICO. *Sonora*: 28 mi. E Mazatán. *Chihuahua*: La Bufa, 3500 ft. *Durango*: Pueblo Nuevo. *Jalisco*: 2 mi. E Bolaños. *Zacatecas*: 1 mi. N Santa Rosa, 3700 ft. *Querétaro*: 8.2 mi. S Peña Blanca; Hda. X-Conca, 2 mi. SSE Conca. *San Luis Potosí*: 10 km. N Tepeyac. *Tamaulipas*: Sierra de Tamaulipas, 16 mi. W, 3 mi. S Piedra, 1400 ft. COLOMBIA. *Guajira*:

Villanueva. *Norte de Santander*: Guamalito. *Antioquia*: San Jeronimo, 720 m. *Valle del Cauca*: La Habana, 20 km. E Buga. *Nariño*: 80 mi. from Buenaventura (Ecuador).

***Glossophaga soricina mutica* Merriam**

1898. *Glossophaga mutica* Merriam, Proc. Biol. Soc. Washington, 12:18, 27 January.

1913b. *Glossophaga soricina mutica*, Miller, Proc. U.S. Nat. Mus., 46:420, 31 December.

Holotype.—Adult male, skin and skull, USNM 89271 (Biological Surveys Collection), from María Madre, Tres Marías Islands, Nayarit, México; obtained on 8 May 1897 by E. W. Nelson and E. A. Goldman, original no. 10976. Holotype examined; skin and skull in excellent condition.

Measurements of the holotype.—Total length, 65 (Merriam, 1898); length of tail, 8 (Merriam, 1898); length of hind foot, 10.4 (Miller, 1913b); length of ear “from anterior basal angle,” 9 (Merriam, 1898); length of forearm (dry), 36.3; greatest length of skull, 22.3; condylobasal length, 20.3; zygomatic breadth, 9.4; mastoid breadth, 9.3; interorbital breadth, 4.2; length of maxillary tooththrow, 7.5; length of mandibular tooththrow (c-m3), 7.9.

Distribution.—Known only from María Madre, María Magdalena, San Juanito, and María Cleofas—Tres Marías Islands (Fig. 27).

Comparisons.—A moderately large race of *G. soricina*, both externally and cranially, but more so in measurements of cranial length (Table 16). *G. s. mutica* can be further characterized by its greatly procumbent upper incisors, shallow basisphenoid pits, and poorly developed postpalatal processes. This race averages paler in color of pelage than does *G. s. handleyi* and *G. s. soricina*, and is similar in color to *G. s. antillarum* and *G. s. valens*.

Remarks.—*G. s. mutica* apparently roosts in caves (Merriam, 1898). Pregnant females have been collected in March and May; lactating females also have been taken in May.

Average external measurements and weight (extremes in parentheses) of 12 males, followed by those of six females, of *G. s. mutica* are: total length, 62.6 (57-80), 62.2 (61-65); length of tail, 6.4 (5-9), 6.3 (5-8); length of hind foot, 10.4 (8-12), 10.0 (8-12); length of ear from notch, 14.1 (13-15), 13.8 (12-15); weight, 9.5 (7-12), 10.5 (9-14).

Specimens examined (33).—MEXICO. *Nayarit*: María Cleofas, 3 (USNM); María Madre, 50-500 ft., 22 (USNM); María Magdalena, 6 (USNM); San Juanito, 2 (USNM).

Marginal records.—MEXICO. *Nayarit*: Tres Marías Islands (see above).

***Glossophaga soricina soricina* (Pallas)**

1766. *Vespertilio soricinus* Pallas, Miscellanea zoologica . . . , p. 48.

1818. *Glossophaga Soricina* É. Geoffroy St.-Hilaire, Mém. Mus. Hist. Nat., Paris, 4:418.

1823. *Glossophaga amplexicaudata* Spix, Simiarum et vespertilionum brasiliensium species novae . . . , p. 66. Type locality unknown.

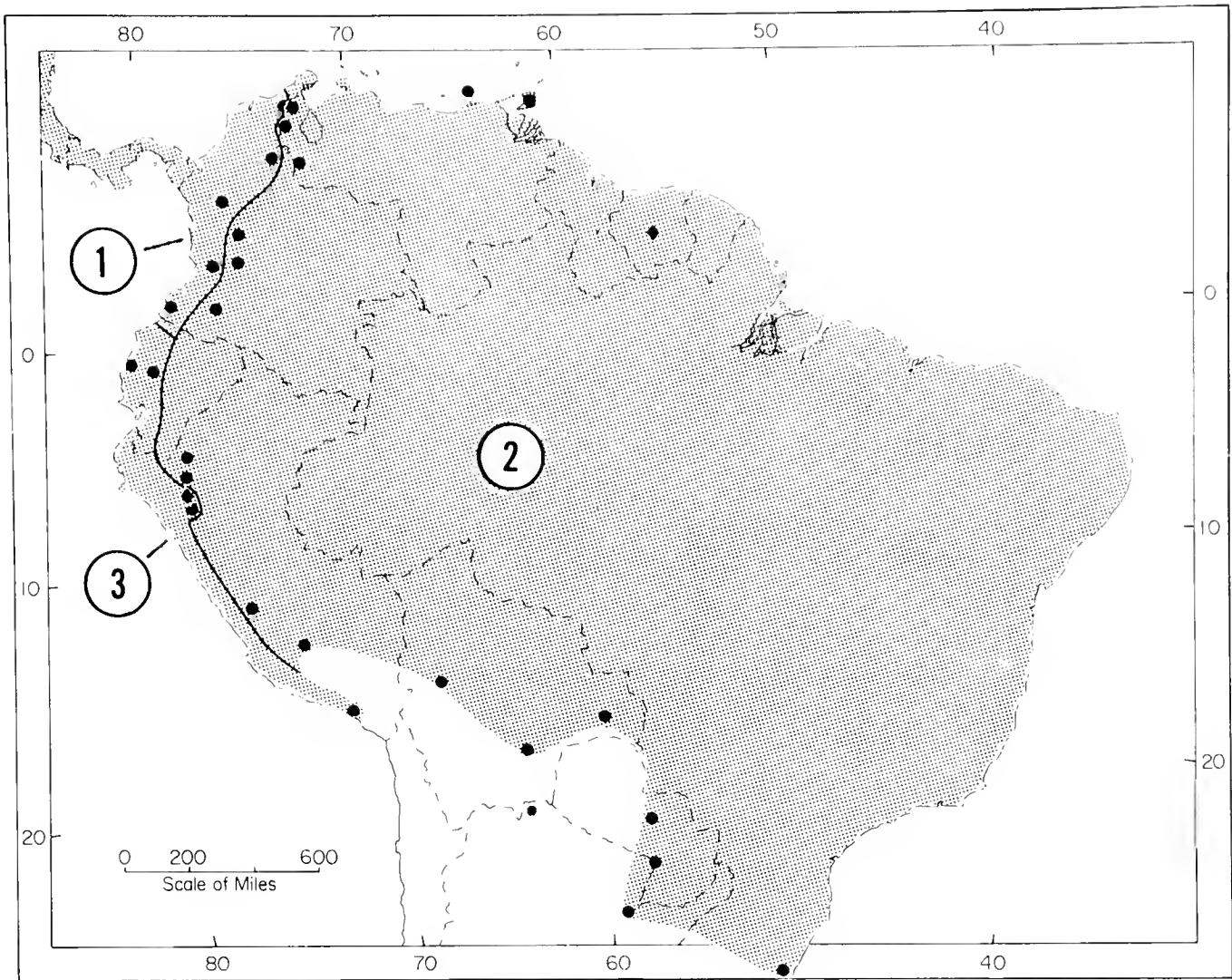


FIG. 28.—Geographic distribution of *Glossophaga soricina* in South America. Recognized subspecies are *G. s. handleyi* (1), *G. s. soricina* (2), and *G. s. valens* (3). Circles represent marginal localities and diamonds represent type localities.

1844. *Phyllophora nigra* Gray, Mammalia, in The zoology of the voyage of the H.M.S. Sulphur..., 1:18, April; holotype from "Tropical America" (=Brazil). (Based on the same specimen as *Phyllophora nigra* Gray, 1843, a *nomen nudum*.)
1896. *Glossophaga villosa* H. Allen, Proc. U.S. Nat. Mus., 18:779, 27 October; holotype from "Guyana, Venezuela" (see Lyon and Osgood, 1909). Name preoccupied by Rengger, 1830.
1897. *Glossophaga truei* H. Allen, Science, N. S., 5:153, 22 January: a renaming of *G. villosa* H. Allen.
- 1913b. *Glossophaga soricina microtis* Miller, Proc. U.S. Nat. Mus., 46:419, 31 December; holotype from Sapucay, Cordillera, Paraguay.

Holotype.—Type specimen, a female, assumed to be lost (Peters, 1866; Carter and Dolan, 1978); type locality restricted to "northern South America" by Rehn (1902a), and listed as "Suriname" by Miller (1912).

Distribution.—From northern South America (east of the Andes) southward to Paraguay and northern Argentina (Barquez, 1985), and on some Caribbean islands (Webster and Handley, 1986) as well (Fig. 28); known altitudinal distribution from near sea level to approximately 2000 meters in elevation.

TABLE 20.—*Recorded reproductive activity in females of Glossophaga soricina soricina.*

Month	Number examined	Number pregnant	Number lactating
January	33	7	5
February	35	12	0
March	50	1	5
April	30	8	6
May	26	1	1
June	50	8	10
July	114	37	4
August	40	11	1
September	31	2	4
October	76	8	8
November	77	9	21
December	54	13	12

Comparisons.—The smallest race of *G. soricina*, both externally and cranially (Table 16). *G. s. soricina* is easily distinguished from the other races of the species by its darker pelage, short and narrow rostrum, moderate rostral slope, and sub-parallel zygoma. Furthermore, the braincase is shallow, domed, and evenly rounded along the posterior border in *G. s. soricina*, rather than squared as in the other races.

Reproduction.—Reproductive information from 537 females (Table 20) indicates that *G. s. soricina* is reproductively active throughout the year, but with two peaks in pregnancy, one from December through February and another in July and August. Average length of testes, followed by sample size in parentheses, of males collected in the months from June through November was 4.0 (7), 4.6 (7), 4.0 (3), 5.5 (1), 6.3 (6), and 2.0 (1). The reproductive strategy of *G. s. soricina*, therefore, is that of monotocous bimodal polyestry, as seen in several other phyllostomids such as some members of the genera *Carollia*, *Uroderma*, *Dermanura*, and *Artibeus* (Wilson, 1979).

Remarks.—See the species account of *Glossophaga soricina* for additional comments concerning the ecology and natural history of this race. Average external measurements (extremes in parentheses) of 46 males, followed by those of 43 females, of *G. s. soricina* are: 62.0 (50-70), 62.6 (54-73); length of tail, 7.5 (4-11), 7.4 (4-11); length of hind foot, 10.1 (7-12), 10.1 (8-12); length of ear from notch, 13.8 (9-17), 13.7 (8-16). Twenty-three males and 13 nonparous females averaged 9.5 (7.5-17) and 8.9 (5-13) grams in weight, respectively.

Specimens examined (876).—BOLIVIA. *El Beni*: Boca Río Baures, 3 (AMNH); 1-24 mi. from Boca Río Ibare, 2 (AMNH); *ca.* Costa Marques (Brazil), 5 (AMNH); 5 km. S Guayaramerín, Río Mamore, 1 (AMNH); La Esperanza, 1 (FMNH); 17 km. NNW Nuevo Berlín, 3 (AMNH); 15 km. SE Puerto Julio, 1 (AMNH); Riberalta, Vacadiez, 1 (USNM); *ca.* Río (Puerto) Acre, 1 (AMNH); 0-20 km. S San Joaquín, 38 (6 AMNH, 32 FMNH); 10 km. W San Pedro, 1 (AMNH); 8 km. N

Santa Cruz, 1 (AMNH); Trinidad, 1 (FMNH). *La Paz*: 4 km. (by road) NW Alcoche, 18 (UMMZ); Caranavi, 606 m., 21 (13 MSU, 8 TTU); Guanay, 2 (AMNH); 1 mi. W Puerto Linares (Santa Ana), Tomonoco, 17 (9 MSU, 8 TTU). *Santa Cruz*: Buena Vista, 3 (AMNH); 7 km. N Santa Rosa, 800 m., 19 (AMNH); Santiago, 3 (FMNH). **BRAZIL**. *Amazonas*: Auara Igarope, Rio Madeira, 14 (AMNH); Boca Tefe, Rio Amazonas, 11 (AMNH); Borba, Rio Negro, 1 (AMNH); *ca.* Manaus, Rio Negro, 3 (AMNH); Mirapinima, Rio Negro, 7 (AMNH); Rosarinho, Rio Madeira, 14 (AMNH); Yucali, Rio Negro, 3 (AMNH). *Bahia*: Formosa do Rio Prêto, 6 (FMNH); Ibipetuba (Santa Rita do Rio Prêto), 8 (FMNH); São Marcelo, Rio Prêto, 3 (FMNH). *Goiás*: Anápolis, 1000 m., 1 (AMNH). *Maranhão*: Alto Parnaíba (Parnahyba), 6 (FMNH); Rosario, 3 (FMNH); São Luís, 2 (USNM). *Mato Grosso*: Arapua, 4 (FMNH); Chavantina, Rio das Mortes, 66 (LACM); Maracaju, 500 m., 3 (AMNH); Recreio, Rio Majary, 11 (AMNH); Serro do Roncador, *ca.* 1750 ft., 3 (USNM); Urucúm, 12 (8 AMNH, 4 FMNH). *Minas Gerais*: 3 mi. ESE Sete Lagoas, 4 (USNM). *Pará*: *ca.* Belém, 2 (USNM); Belterra, Rio Tapajos, 1 (FMNH); *ca.* 10 km. NW Bragança, 3 (USNM); Faro, Rio Amazonas, 22 (AMNH); Igarabé Brabo, Rio Tapajos, 4 (AMNH); Ilha do Taiuna, Rio Tocantins, 25 (AMNH); Mocajuba, Rio Tocantins, 3 (AMNH); Rio Nhamundá (Jamundá), 2 (FMNH); Rio Tapajos, 13 (AMNH); Rio Tocantins, 2 (FMNH); Santarém, Rio Amazonas, 2 (FMNH); Tauari, Rio Tapajos, 13 (AMNH); Vilarinho do Monte, Rio Xingu, 6 (AMNH); no locality, 3 (CMNH). *Piauí*: Derserto, 6 (FMNH). *Rio Grande do Norte*: Natal, 1 (CAS). *Rondônia*: Pôrto Velho, Rio Madeira, 20 (LACM). *Roraima*: Boa Vista, Rio Branco, 1 (FMNH). *São Paulo*: Barra do Rio Dourado, 2 (FMNH); Barra do Rio Juquiá (Jugíá), 1 (FMNH); São Sebastião (San Sebastian), 4 (2 FMNH, 2 USNM). **COLOMBIA**. *Amazonas*: 30 km. NW Leticia, Isla Santa Sofia, 1 (TTU). *Cundinamarca*: Boquerón (Bogotá), 2 (FMNH). *Huila*: Pitalito, 1 (FMNH); Timaná, 1250 m., 8 (FMNH). *Tolima*: Honda, 1 (AMNH); Mariquita, 1 (AMNH). **ECUADOR**. *Napo*: Santa Cecilia, 5 (1 KU, 1 MSU, 3 TTU). **FRENCH GUIANA**. *Saint-Laurent-du-Maroni*: Saül, 1 (KU). **GUYANA**. *East Berbice-Corentyne*: Berbice, 1 (USNM); Canje, 19 (AMNH); 5 mi. SSW Ituni, 1 (ROM). *East Demerara-West Coast Berbice*: Georgetown, 6 (2 AMNH, 2 FMNH, 2 ROM); Kartabu (Kartabo), 1 (AMNH); west bank Demerara River, 5 (2 AMNH, 3 FMNH). *Rupununi*: Achimeriwau (Achamere Wau Head), 1 (ROM); Nappi Creek, *ca.* Lethem, 3 (ROM); upper Sawariwau River, 1 (ROM); Wee Wee Tau, 20 mi. E Dadanawa, 10 (ROM). *West Demerara-Essiquibo Coast*: Phoenix, Leguan, Essiquibo River, 2 (AMNH). **PARAGUAY**. *Amambay*: Parque Nacional Cerro Corá, 1 (UMMZ); 20 km. SW Pedro Juan Caballero, 1 (UMMZ). *Caroveny*: Villarrica, 2 (AMNH). *Central*: Asunción Recoleta, 2 (UMMZ). *Cordillera*: 1 mi. S Tobatí, 9 (MVZ). *Guiará*: Villarica, 11 (6 AMNH, 5 USNM). *Itapúa*: 22 km. (by road) NNE Encarnación, 1 (UMMZ). *Paraguarí*: 17 km. (by road) SW Piribebuy, 1 (UMMZ); Sapucay (Sapucaí), 6 (USNM). *San Pedro*: Rückenau, Friesland Colony, Itacurubi del Rosario, 2 (KU). **PERU**. *Amazonas*: *ca.* 0.5 mi. W Huampani, Río Cenepa, 4 (MVZ); La Poza, Río Santiago, 180 m., 1 (MVZ); 12 mi. SSW Nazareth, 1100 ft., 2 (MVZ). *Cuzco*: Idma, 6000 ft., 1 (USNM); Valle de Convención, 2 (FMNH). *Huánaco*: Tingo Maria, 1 (LSU). *Junín*: Chanchamayo, 2 (FMNH); Río Ene, 340 m., 1 (OU); Tarma, 2 mi. SW San Ramon, 2900 ft., 6 (AMNH). *Loreto*: Boca Río Curaray, 3 (AMNH); Boca Río Peruete, Río Amazonas, 1 (FMNH); Esperanza, Río Yavari-Mirim, 2 (FMNH); Iquitos, 2 (AMNH); Lagarto, Alto Ucayali, 1 (AMNH); Moyobamba (Moyombamba), 8 (FMNH); Naute, Río Samiria, Sante Elena, 1 (FMNH); Orosa, Río Amazonas, 5 (AMNH); Pucallpa, 7 (FMNH); Río Apayacu, 1 (AMNH); Río Curanja, Balta, *ca.* 300 m., 9 (LSU); Ucayali, 59 km. SW Pucallpa, 2 (USNM); Yarina Cocha (Yarincocha), 4 (LSU). *Madre de Dios*: Maldonado, 1 (FMNH); Río Azul (Boca Río Shilivi), 1 (FMNH). *Pasco*: Oxapampa, Nevati Mission, 900 ft., 7 (AMNH); Oxapampa, San Juan, 900 ft., 3 (1 AMNH, 2 USNM); Oxapampa, San Pablo, 900 ft., 1 (AMNH); no locality, 3 (AMNH). *San Martín*: upper Huallaga, Pachiza, 1 (AMNH). *No locality*: 1 (AMNH). **SURINAME**. *Nickerie*: Avanavero, Sipaliwini Airstrip, 6

(CMNH). *Para*: Lelydorpplan, 7 (FMNH); Zanderij (Zandery), 2 (CMNH). *Paramaribo*: Paramaribo, Keizerstraat 232, 2 (CMNH). **TRINIDAD**. *Caroni*: Tabaquite, Río Claro, 1 (AMNH). *Mayaro*: Guayaguayare, 30 (1 AMNH, 29 TTU). *Nariva*: 5 mi. Mark Plum Mitán Road, 4 (TTU). *St. Andrew*: Cumuto (Cumlito), 1 (UMMZ); Tamana, Monceaux Estate, 1 (AMNH); 2 mi. N Jct. Turre and Eastern, 3 (OU); 2 mi. N, 2 mi. W Valencia, 7 (TTU). *St. George*: Blanchisseuse Valley, 19 (1 KU, 18 TTU); Cascada, 1 (OU); Las Cuevas, 14 (2 CMNH, 2 KU, 10 TTU); Maracas Valley, 3 (TTU); Port of Spain, 5 (UMMZ); San Rafael (Rafael), 9 (TTU). *St. Patrick*: Granville, 1 (AMNH); Green Hill, Cedros, 1 (AMNH); Point Fortin, 1 (AMNH). *Victoria*: Tableland, North Road, 1 (AMNH). *County unknown*: south Trinidad, 1 (LSU). **VENEZUELA**. *Apure*: San Fernando (de Apure), 400 ft., 1 (AMNH); 41 km. NW Puerto Páez, 1 (USNM). *Aragua*: Rancho Grande, 1 (UMMZ). *Bolívar*: Aroa (Pueblo Nuevo), 3 (AMNH); El Callao, Peru Mine, 14 (AMNH). *Carabobo*: San Esteban, 3 (1 AMNH, 2 USNM); 2.5 km. NW Urama, 16 (USNM). *Distrito Federal*: Caracas, 2 (AMNH); *ca.* El Limón, 3 km. S, 46 km. W Caracas, 1 (USNM); Guaira (Guayra), 1 (USNM); Los Venados, 5 km. N Caracas, 1555 m., 2 (USNM); San Julián, 5 (USNM). *Falcón*: 35 km. NW Puerto Cabello, Boca de Yaracuy, 2 m., 2 (USNM). *Miranda*: *ca.* Puerto Tuy, 5 km. E Río Chico, 1 m., 1 (USNM); Santa Crucita Campground, Parque Nacional de Guatopo, 500 m., 1 (USNM); Santa Lucía, 3 (CMNH); *ca.* Turgua, 8 km. S Caracas, 1144 m., 1 (USNM). *Sucre*: 2.5 km. SE Cumaná, 10 m., 4 (KU). *T. F. Amazonas*: San Juan, Río Manapiare, 155 m., 4 (USNM). *Trujillo*: Agua Santa, 23 km. SW Valera, 6 (USNM); *ca.* Agua Viva, 18-22 km. N Valera, 164 m., 7 (USNM). *Yaracuy*: 19 km. NW Urama, 10 (USNM). *Zulia*: 10 km. S, 18 km. W Machiques, 270 m., 5 (USNM); 3 km. S, 19 km. W Machiques, 1135 m., 1 (USNM). *Territory or state unknown*: Auxantepui, 460 m., 7 (AMNH); Oramo, 1 (USNM).

Selected additional records.—**ARGENTINA**. *Chaco*: Resistencia [*fide* Podtiaguin (1944), who cited Denier (date of publication unknown) and Veizel (date of publication unknown)]. *Salta*: Quebrada de Tartagal, Finca Abra Grande (Barquez, 1985; Ojeda and Mares, 1989). **BOLIVIA** (Anderson *et al.*, 1982, unless otherwise noted). *Chuquisaca*: 70 km. SE Padilla, along Río Azuero, 1100 m. *Cochabamba*: *ca.* Villa Tunari. *El Beni*: Aguadulce; Barranquita; Centenela; El Mojón; Estación Biológica Beni (Cabot *et al.*, 1986; Wilson and Salazar, 1989); Magdalena; Rurrenabaque; Tumi Chucua (Webster and Fugler, 1984); Veinte y Dos, Yuatre, 25 km. SW San Joaquín. *Santa Cruz*: 6 km. S, 10 km. E Comarapa; 10 km. E Gutiérrez, Laguna Caucaya; 7 km. E Ingeniero Morá; La Laguna, 10 km. N San Ramón (Ibañez, 1985); Pampa de la Isla (Santa Cruz de la Sierra). **BRAZIL** (da Cunha Vieira, 1942, unless otherwise noted). *Amapá* (de Carvalho, 1962): Amapá; Macapá. *Amazonas*: Itacoatiara; Rio Juruá; Silves. *Bahia*: Barra; Barrinha; Fazenda Flamengo, km. 150 on Route BA 130 (Mares *et al.*, 1981); Fazenda Morro da Imburana, km. 145 on Route BA 130 (Mares *et al.*, 1981); Ilha Madre Deus; Ilhéus; Pilão Arcado; *ca.* Salvador (Morrison and McNab, 1967); Vila Nova. *Ceará*: Cerro de Castillo (Thomas, 1920); within 21 km. Crato (Mares *et al.*, 1981); 4 km. SE Nova Olinda, km. 19 on Route CA 96 (Mares *et al.*, 1981); Russo. *Espírito Santo*: Gruta do Rio Itaúnas (Ruschi, 1953); Rio Doce. *Goiás*: Rio das Mortes. *Maranhão*: Maranhão (Miller, 1913b); Vila Braga (Thomas, 1920). *Mato Grosso*: Rondonópolis; Santa Ana do Parnaíba; S. Luiz de Cáceres; 264 km. (by road) N Xavantina, Serro de Roncador (Pine *et al.*, 1970). *Minas Gerais*: Benjamin Constant; Paraopeba; Pirapora; Teófilo Otoni. *Pará*: Abaeté; Baião, Rio Tocantins (Miller, 1913b); Buiussú; Catema, Rio Tocantins (Miller, 1913b). *Paraná*. *Pernambuco* (Mares *et al.*, 1981): within 21 km. Exu; Estação Ecológica de Tapacurá; Fazenda Salto, 35 km. NNE Serro Talhada. *Piauí* (Mares *et al.*, 1981): km. 18 on Route BA 316; within 5 km. Valença do Piauí. *Rio de Janeiro*: Rio de Janeiro. *Rio Grande do Sul* [*fide* da Cunha Vieira (1942), who cited von Ihering (1895)]: Pôrto Alegre; São Lourenço. *Santa Catarina*. *São Paulo*: [over 50 additional records are in da Cunha Vieira (1942) and Taddei (1975)]. **COLOMBIA**. *Cundinamarca*: Cachipay, 1585 m. (Valdivieso, 1964); El Colegio (Mesitas del Colegio), 1210 m.

(Tamsitt and Valdivieso, 1963, 1964); Giradot (Tamsitt and Valdivieso, 1963, 1964); La Mesa, 1298 m. (Valdivieso, 1964); Paramo de Choachi (Anthony, 1923). ECUADOR (Albuja, 1983, unless otherwise noted). *Napo*: Bobonata; Cavernas de Jumandi; Límon Cocha (Baker, 1974); San Pedro de los Cofanes. FRENCH GUIANA (Brosset and Dubost, 1967). *Cayenne*: Cayenne. *Saint-Laurent-du-Maroni*: Mana. LESSER ANTILLES (Webster and Handley, 1986). *Grenada*. *Grenadines*: Bequia. PARAGUAY. *Concepción*: Concepción (Bertoni, 1939); 8 km. (by road) E Concepción (Myers and Wetzel, 1983). *Presidente Hayes*: Puerto Cooper (Podtiaguín, 1944). PERU. *Huánaco* (Koopman, 1978); Cerros del Sira, 1120 m.; Tournavista. *Loreto*: Indiana (Pirlot, 1968); Pebas, 330 ft. (Thomas, 1920). *Pasco*: Villa Rica, 2000 m. (Pirlot, 1968). SURINAME (Husson, 1962, unless otherwise noted). *Brokopondo*: Brownsberg Nature Park, 6 km. S, 20 km. W Afobaka (Genoways and Williams, 1979b); Leonsberg (Lukoschus *et al.*, 1973); 1.5 km. W Rudi Kappelvliegveld, 330 m. (Williams and Genoways, 1980). *Marowijne*: Galibi, mouth of Marowijne River; coastal region between Moengotapoe and Wiawia Bank. *Nickerie*: Frederik Willem IV Falls, Corantijn River. *Para*: Republiek. *Saramacca*: Tijger Kreek, Saramacca River. VENEZUELA (Handley, 1976, unless otherwise noted). *Barinas*: Altamira, 609-1070 m. *Bolívar*: 8 km. W El Manteco (Haiduk and Baker, 1982). *Delta Amacuro*: Guayo (Pirlot, 1965). *Guárico*: 45 km. S Calabozo (Baker *et al.*, 1981; Honeycutt and Sarich, 1987; Honeycutt *et al.*, 1981); Embalse de Guárico, 10 km. N Calabozo, 100 m.; Hato Las Palmitas, 35 km. SSW San Juan de los Morros, 181 m. *Lara*: Caserio Boro, 10 km. NE El Tocuyo, 580 m. *Miranda*: Birongo, 60 m. *Monagas*: Hato Mata de Bejuco, 55 km. SSE Maturín, 18 m.; San Agustín, 3-5 km. NW Caripe, 175-1175 m. *Nueva Esparta*: Isla Margarita, 10 km. WSW La Asunción, 47 m.; Isla Margarita (Pirlot and León, 1965). *Táchira*: Las Mesas, 17 km. NE San Juan de Colón, 460 m.

Marginal records.—VENEZUELA. *Nueva Esparta*: Isla Margarita. TRINIDAD. BRAZIL. *Rio Grande do Sul*: Pôrto Alegre. ARGENTINA. *Chaco*: Resistencia. PARAGUAY. *Central*: Ascunción Recoleta. *Presidente Hayes*: Puerto Cooper. BOLIVIA. *Santa Cruz*: Santiago. *Chuquisaca*: 70 km. SE Padilla, along Río Azuero, 1100 m. ARGENTINA. *Salta*: Quebrada Tartagal, Finca Abra Grande. BOLIVIA. *La Paz*: Caranavi, 606 m. PERU. *Cuzco*: Idma, 6000 ft. *Junín*: Tarma, 2 mi. SW San Ramon, 2900 ft. *Amazonas*: 12 mi. SSW Nazareth; ca. 0.5 km. W Huampani, Río Cenepa. COLOMBIA. *Huilia*: Pitalito. *Cundinamarca*: Giradot. *Tolima*: Honda. VENEZUELA. *Táchira*: Las Mesas, 17 km. NE San Juan de Colón, 460 m. *Zulia*: 3 km. S, 19 km. W Machiques, 1135 m.; near Cerro Azul, 33-35 km. NW La Paz, 75-80 m.

Glossophaga soricina valens Miller

1913b. *Glossophaga soricina valens* Miller, Proc. U.S. Nat. Mus., 46:420, 31 December.

Holotype.—Adult female, skin (in alcohol) and skull, FMNH 19868, from Balsas, Amazonas, Perú; obtained on 16 May 1912 by W. H. Osgood and M. Anderson, original no. 4723. Holotype examined; right forearm and third and fourth metacarpals damaged, pelage extremely faded, skull in excellent condition.

Measurements of the holotype (external measurements except forearm by Miller, 1913b.).—Length of head and body, 55; length of tail, 8; length of hind foot, 10; length of ear from meatus, 15; length of forearm, 39.8; greatest length of skull, 22.0; condylobasal length, 20.8; zygomatic breadth, 9.7; mastoid breadth, 9.1; interorbital breadth, 4.2; length of maxillary tooththrow, 7.8; length of mandibular tooththrow (c-m3), 8.3.

Distribution.—Known from the west coast of South America at least from Manabí, Ecuador, southward to Arequipa, Perú, and eastward into the upper Río Marañón drainage of Amazonas, Perú (Fig. 28); known altitudinal distribution from near sea level to 1025 meters in elevation.

Comparisons.—A large race (Table 16) of *G. soricina* that exhibits clinal variation in external and cranial dimensions and pelage coloration; specimens from the southern part of the distribution are massive and pale, whereas those to the north are relatively small and dark. Specimens of *G. s. valens* are immediately distinguished from those of *G. s. handleyi* and *G. s. soricina* by their large overall size, extremely procumbent upper incisors, anteriorly converging zygoma, and gradually sloping rostra. It is difficult, however, to distinguish specimens of *G. s. valens* from those referable to *G. s. antillarum* and *G. s. mutica* by size alone, but the isolated geographic distribution of these taxa suggests that no gene flow occurs between them.

Remarks.—Albuja (1983) reported *G. s. valens* from two coastal localities in northwestern Ecuador (San Borenzo and Urbina in Esmeraldas) and Dorst (1951) noted the occurrence of *G. soricina* at La Tola (Esmeraldas). These specimens come from a zone of intergradation between *G. s. handleyi* and *G. s. valens*. Specimens examined by me from west-central Ecuador (Manabí and Los Ríos), although closer overall to *G. s. valens*, exhibit many of the characteristics of *G. s. handleyi*, whereas those from southwestern Colombia (Nariño and Valle del Cauca) are clearly assignable to *G. s. handleyi*. Since I have not examined individuals from Esmeraldas, I have not included those records in either account.

Little is known about the natural history of *G. s. valens*. This bat inhabits the xeric west coasts of Ecuador and Perú, and has become established in the arid upper Río Marañón Valley as well. It has been collected from caves, and is known to share daytime roosts with *Amorphochilus schnablii* (Ortiz de la Puente D., 1951). Pregnant females have been taken in September, and lactating females are known from March, June, August, September, and October.

Average external measurements (extremes in parentheses) of 16 males, followed by those of 21 females, of *G. s. valens* are: total length, 65.9 (58-74), 67.8 (61-90); length of tail, 6.8 (5-10), 7.8 (6-10), length of hind foot, 10.8 (10-12), 10.7 (9-12); length of ear from notch, 14.0 (12-16.5), 15.3 (8-16). Eleven males and nine non-parous females averages 9.1 (6-12.5) and 9.5 (8-11) grams in weight, respectively.

Specimens examined (186).—ECUADOR. *El Oro*: Portovelo, 2000 ft., 1 (AMNH); Portovelo, 1.5 mi. S Zaruma, 2800 ft., 3 (TCWC); Santa Rosa, 100 ft., 3 (AMNH); 9 mi. S Zaruma, 2000 ft., 3 (TCWC). *Guayas*: Daule, 6 (AMNH); Durán, sea level, 8 (AMNH); Guayaquil, 1 (AMNH); Huerta Negra (near Tenguel), 20 km. ESE Balao, 7 (USNM); Isla Puná, San Ramón, 1 (AMNH); Manglaralto, 10 (4 AMNH, 6 UMMZ); Manglaralto, Cordillera de Colonche, 3 (UMMZ); San Rafael, 7 km. S Balao, 13 (USNM). *Loja*: Malacatos, 4 (FMNH). *Los Ríos*: El Papayo (near San Juan), 7 km. SW Pueblo Viejo, 6 (USNM); Lima Pareja (near San Juan), 4 km. SW Pueblo Viejo, 14 (USNM). *Manabí*: Bahía de Caráquez, Río Briseño, 1 (AMNH). PERU. *Amazonas*: Bagua, Hda. Valor, ca. 1100 ft., 6 (LSU); 8-10 km. WSW Bagua, 1500-1700 ft., 6 (MVZ); Balsas (along Río

Marañón), *ca.* 2700 ft., 6 (3 FMNH, 3 LSU). *Ancash*: 28 km. SE Huarney, 1 (LSU); Pariacoto, Huaraz, 3 (FMNH). *Arequipa*: Tambo Valley, Hda. Chucarapi, 1 (FMNH). *Ayacucho*: Río Santa Rosa, San José, *ca.* 3300 ft., 2 (LSU). *Cajamarca*: El Arenal, 1 km. S, 6 km. W Pomahuaca, 3000 ft., 4 (MVZ). *Lambayeque*: Chongoyape, 9 (FMNH); Mórrope, 100 ft., 3 (MVZ); Motupe, 1 (FMNH); 4 mi. SSW Motupe, 400 ft., 2 (MVZ); Olmos, 7 (FMNH); 12 km. N Olmos, *ca.* 500 ft., 2 (MVZ). *Lima*: Cañete, 22 (LSU); Naña, 2 (FMNH). *Piura*: Charapex, 4 (USNM); Salitral, 1 (FMNH); Sullana, 6 (FMNH); *ca.* 90 km. NNW Sullana el Angolo, *ca.* 700 m., 3 (LSU); 4 mi. W Suyu, 1000 ft., 1 (TCWC). *Tumbes*: 5 km. E Puerto Pizarro, 4 (LSU); Rica playa, Río Tumbes, 2 (LSU); no locality, 3 (FMNH). *No locality*: 1 (USNM).

Additional records.—ECUADOR (Albuja, 1983, unless otherwise noted). *El Oro*: Arenillas. *Manabí*: Chontillal; Manabí (J. A. Allen, 1916). *Los Ríos*: Pacaritambo (Brosset, 1965); Quevedo. PERU (Ortiz de la Puente D., 1951, unless otherwise noted). *Ica*. *La Libertad*. *Lima*: Atocongo, 200 m. (Barquez, 1984); Lima. *Piura*: Talara. *Tumbes*: Zorritos (G. M. Allen, 1908).

Marginal records.—ECUADOR. *Manabí*: Bahía de Caráquez, Río Briseño. *Los Ríos*: Quevedo. PERU. *Amazonas*: Bagua, Hda. Valor, *ca.* 1100 ft.; Balsas. *Arequipa*: Tambo Valley, Hda. Chucarapi.

SPECIFIC RELATIONSHIPS

The relationship among the five species of *Glossophaga* relative to the morphology of the cranium, teeth, hair, chromosomes, isozymes, and current patterns of distribution are discussed below. These biological characteristics are synthesized with quantitative data in the following chapter in order to detail evolutionary relationships among species of the genus.

In writing this chapter, it was convenient to have at hand typical adult specimens of each of the five species. These were used as reference points for certain detailed comparisons, and they could prove to be useful to future workers as a point of departure in identifying specimens or verifying specific characteristics. The specimens selected as typical representatives of the five species were: *G. commisaris* (TTU 36125, from 8.2 mi. NE, 2.5 mi. E Tonalá, Río Ocuilapa, Chiapas, México); *G. leachii* (TTU 36127, from 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa, Chiapas, México); *G. longirostris* (TTU 35695, from 0.75 km. S, 0.5 km. W Concord, St. John, Grenada); *G. morenoi* (TTU 36142, from 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa, Chiapas, México); and *G. soricina* (TTU 18418, from 8 mi. N, 5.5 km. E Playa del Carmen, Quintana Roo, México).

Cranial Morphology

Pterygoid alae, presphenoid ridge, basisphenoid pits, slope of rostrum, and postpalatal processes were qualitative characters examined in each species of *Glossophaga*. Although there is variation in each of these characters, more of it geographic than individual, some are species-specific, and identifications frequently can be made on the basis of cranial morphology even when specimens lack teeth.

Pterygoid alae are absent in *G. commissarisi* and *G. longirostris*, absent or only poorly developed in *G. morenoi*, and well developed in *G. leachii* and *G. soricina*. The presphenoid ridge is high and complete throughout in *G. leachii*, *G. longirostris*, and *G. soricina*, but it is flattened subterminally in *G. commissarisi* and *G. morenoi*. Basisphenoid pits exhibit considerable variation in all species of *Glossophaga*, but in general the pits are much shallower in *G. soricina* than in other congeners. The slope from rostrum to braincase is also highly variable, particularly in the polytypic *G. longirostris* and *G. soricina*. Overall, however, specimens of *G. longirostris* and *G. morenoi* generally have a gradual rostral slope, those of *G. commissarisi* and *G. leachii* have a noticeable slope from rostrum to braincase, and the slope in *G. soricina* varies tremendously geographically. The postpalatal processes exhibit so much individual and geographic variation that they cannot be used to distinguish among species.

Two other morphological characters are useful in identifying specimens of *Glossophaga*, but they were not examined by me as qualitative characters until after this investigation was underway. The mandibular symphyseal ridge is well developed and forms a distinct “chin” in *G. commissarisi*, *G. leachii*, and *G. soricina*; this ridge is absent in *G. longirostris* and poorly developed in *G. morenoi*. Also, the premaxillaries are noticeably elongate in species with procumbent upper incisors—*G. longirostris*, *G. morenoi*, and *G. soricina*—but evenly rounded between the canines in *G. commissarisi* and *G. leachii*.

Dental Morphology

The five species of *Glossophaga* can be identified most easily by examining the morphology of the upper and lower teeth. Some teeth, however, are more diagnostic than others; those most useful are noted below.

The upper incisors are variable in morphology in all species of *Glossophaga*, but in general those of *G. commissarisi*, *G. leachii*, *G. longirostris*, and *G. morenoi* more closely resemble the upper incisors of each other than any resembles those of *G. soricina*. Specimens of the four species have upper incisors that are essentially equal in bulk, whereas individuals of *G. soricina* have unequal upper incisors, the inner tooth larger because its cutting face is greatly expanded distally (Fig. 29). The cingulum of the outer upper incisor is better developed in *G. commissarisi* and *G. leachii* relative to that condition in *G. longirostris*, *G. morenoi*, and *G. soricina*. In addition, the upper incisors are noticeably procumbent in *G. longirostris*, *G. morenoi*, and *G. soricina*, whereas those of *G. commissarisi* and *G. leachii* tend to be much less procumbent.

The fourth upper premolar has a distinct posterolabial cingulum in *G. commissarisi*, *G. leachii*, and *G. soricina*, resulting in upper premolars that are unequal in bulk, the third being smaller. The upper premolars are similar in size and shape in *G. longirostris*. Specimens of *G. morenoi* have upper premolars that are unequal in

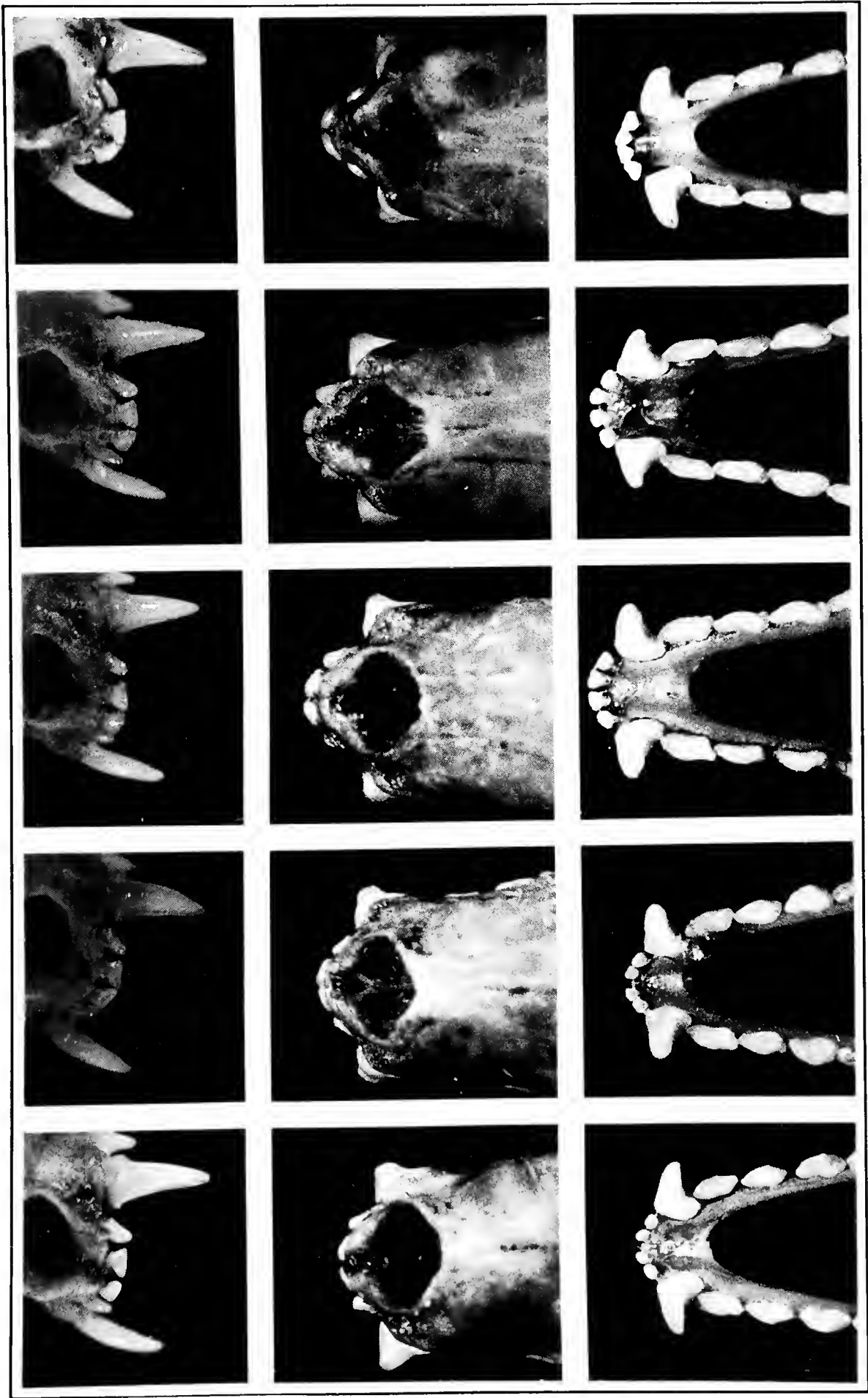


FIG. 29.—Incisor morphology in five species of *Glossophaga*. Oblique and dorsal views of the anterior rostral region, and a dorsal view of the anterior mandibular region, in a typical specimen of, from left to right, *G. commissarisi*, *G. leachii*, *G. longirostris*, *G. morenoi*, and *G. soricina* (see text for identity of individual specimens). Note differences in positioning and morphology of the upper and lower incisors.

bulk (P4 larger than P3), but the cingulum of P4 is not as greatly developed as compared to those of *G. commissarisi*, *G. leachii*, and *G. soricina*.

The upper molars are excellent tools for identifying specimens of *Glossophaga* (Webster and Jones, 1980: fig. 4). In specimens of *G. commissarisi*, the parastyle of M1 is directed labially to posterolabially from the paracone, the fourth commissure of M1 is long and well developed, the parastyle of M2 is directed labially from the paracone, and M3 is relatively small. Specimens of *G. leachii* are characterized by the loss or extreme reduction of the parastyle and mesostyle of M1, the loss of the mesostyle of M2, and a relatively small M3. Bats referable to *G. longirostris* lack the parastyle and mesostyle of M1, lack the mesostyle of M2, and have a relatively large M3. Specimens of *G. morenoi* have a reduced parastyle of M1, the parastyle of M2 is directed posterolabially and forms a distinct notch in the labial outline of the tooth, and M3 is relatively large. The parastyle of M1 is well developed and directed anterolabially in *G. soricina*, the mesostyles of M1 and M2 are well developed, the fourth commissure of M1 is short, and M3 is reduced in size.

The lower incisors are another excellent clue as to the specific identity of bats in this genus (Fig. 29). Specimens of *G. commissarisi* have extremely small, peglike lower incisors that, although widely spaced, are paired with a larger gap between the left and right pairs than between the teeth in each pair; the outer tooth is larger than the inner in bulk; and all teeth are subcircular in occlusal view. The lower incisors in *G. leachii* are small, subtriangular in occlusal view, and usually are paired, the median gap exceeding the diastema between the teeth in each pair. The lower incisors in *G. morenoi* are moderate in size, evenly spaced between the canines, the outer pair slightly larger than the inner in bulk. The large lower incisors in *G. longirostris* and *G. soricina* are usually in contact, particularly in *G. soricina* because the teeth are extremely crowded between the canines.

The lower postcanine teeth are less variable in size and shape than those above, and interspecific variation is minimal. Nevertheless, the lower premolars are smaller in bulk overall in *G. commissarisi* and *G. soricina* relative to those of *G. leachii*, *G. longirostris*, and *G. morenoi*. In addition, the lower premolars are subequal in size in *G. longirostris*, but p4 is distinctly larger than p2 and p3 in *G. commissarisi*, *G. leachii*, *G. morenoi*, and *G. soricina*. The lower molars are larger overall in *G. longirostris* and *G. morenoi* than in *G. commissarisi*, *G. leachii*, and *G. soricina*.

Hair Morphology

Hair was removed from the interscapular region from the specimens mentioned above, and a scanning electron microscope was used to examine the structure. Hair morphology is virtually identical in all five species of *Glossophaga*. The scales are petal-shaped, smooth, imbricate, and two scales surround the shaft of the hair at any given height. Except in the shield region where the scales cling to the shaft, the dis-

tal portion of each scale flares outward from the shaft, especially in the basal part of the hair. Scale length varies slightly in each species, but overall the scales of *G. leachii* are somewhat shorter than those of *G. commissarisi*, *G. longirostris*, *G. morenoi*, and *G. soricina*.

Karyology

The standard karyotypes of *Glossophaga commissarisi*, *G. leachii*, *G. longirostris*, and *G. soricina* were described by Baker (1967, 1979). The four species have identical diploid (32) and fundamental (60) numbers. All autosomes are biarmed (metacentric to approaching subtelocentric) and range in size from large to small; the X-chromosome is a medium metacentric and the Y is a minute acrocentric (Baker, 1979).

The standard karyotype of an adult male *Glossophaga morenoi mexicana* (TTU 36136, from 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa, Chiapas, México) appears identical with those of the other species in the genus (see Baker, 1979:pl. 23). Evidently there has been little chromosomal evolution in the five species of *Glossophaga*, although G- and C-banded chromosomes of the five species have not been compared.

Chromosomal data indicate that members of four other glossophagine genera (*Brachyphylla*, *Erophylla*, *Monophyllus*, and *Phyllonycteris*) have G- and C-banded chromosomes that are indistinguishable from those of *Glossophaga soricina*, the only species in the genus for which chromosomes have been banded. Also, the banded karyotype of *Leptonycteris* is similar to that of *G. soricina*, except that the smallest pair of autosomes is relatively larger in *Leptonycteris* (Haiduk and Baker, 1982). The 2N=32, FN=60 karyotype, therefore, probably is primitive for the entire glossophagine clade (Baker and Bass, 1979; Baker *et al.*, 1981; Haiduk and Baker, 1982).

Biochemical Genetics

Two of 17 isozymes (Idh-2 and Ldh-2) examined in this analysis were monomorphic for all species of *Glossophaga* and the four genera used as outgroups (*Monophyllus*, *Leptonycteris*, *Choeronycteris*, and *Lonchophylla*). Fixed alleles at three loci (Pep-2, Mpi, and α -Gpd) separated the genus *Glossophaga* from the outgroup genera, and indicate the former is a natural assemblage of taxa that is distinct from *Monophyllus*, *Leptonycteris*, *Choeronycteris*, and *Lonchophylla*. This distinction between *Glossophaga* and *Monophyllus* is particularly noteworthy because Varona (1974) considered the two to be congeneric.

One locus (Alb) was fixed for different alleles between *G. morenoi* and the other four species of *Glossophaga*, and another locus (Pep-1) was fixed for different alleles between *G. soricina* and the remaining four species. The maxtrix of Rogers'

similarity values (Table 21) was calculated from the allozyme frequencies of the 15 polymorphic and polytypic loci (Table 22), and a similarity phenogram between OTUs is presented in Figure 30.

The specimens of *Glossophaga* cluster into two groups. Populations of *G. soricina* (7-20) are clearly distinct from those of *G. leachii* (1), *G. morenoi* (3), *G. longirostris* (4-6), and *G. commissarisi* (2). Furthermore, specimens of *G. leachii*, *G. longirostris*, and *G. morenoi* more closely resemble each other biochemically than any of them resembles *G. commissarisi*. All populations of *G. soricina* are identical in allelic content at 89 percent or more of their loci.

Conspecific populations usually share at least 85 percent of their loci; this presents a problem in recognizing subspecies because polymorphic loci are frequently heterozygous and fixed allele differences are rare (Avice, 1975). *Glossophaga soricina* demonstrates this problem in that races that are morphologically (and sometimes geographically) distinct are not discernible by electrophoresis inasmuch as no fixed differences in allelic content were detected. Conversely, levels of biochemical similarity between *G. morenoi* and *G. longirostris* (approximately 89 percent) are well within the range of conspecific animals (for review, see Avice, 1975), but fixed allele differences between *G. morenoi* and the other four species of *Glossophaga* indicate that hybridization does not occur.

Although the genic differentiation among the species of *Glossophaga* is low relative to that characteristic of most closely related mammalian species (Avice, 1975), a similar situation has been found for several taxa of *Dermanura* (a composite referred to as *Artibeus cinereus*, *A. phaeotis*, *A. toltecus*, and *A. watsoni*). There were few fixed allozymic differences among these taxa, although levels of polymorphism and heterozygosity were well within the limits of variation for other phyllostomid species (Koop and Baker, 1983). Not all congeners within the Phyllostomidae are genetically so similar. In seven species of *Tonatia* and eight species of *Micronycteris*, most were distinguished by numerous fixed allelic differences (Arnold, 1981). It is unclear at this time whether the lack of genic differentiation in *Glossophaga* and *Dermanura* is the result of these species being the product of a recent radiation, or if they have undergone a relatively slow rate of genic evolution.

Two other points deserve comment. The small sample size ($N=4$) of *G. commissarisi* probably does not provide an accurate assessment of the total heterozygosity from throughout the range of the species, particularly considering the disjunct distribution and ostensible lack of gene flow between races. This could result in an erroneous coefficient of similarity between *G. commissarisi* and the *leachii-longirostris-morenoi* complex. However, other studies (Gorman and Renzi, 1979; Sarich, 1977) have shown that no significant changes in *S*-values would be expected if the sample size was increased. Secondly, the allozyme data for *G. longirostris major* from Venezuela (Guárico) was indistinguishable from that of *G. l. rostrata* from the

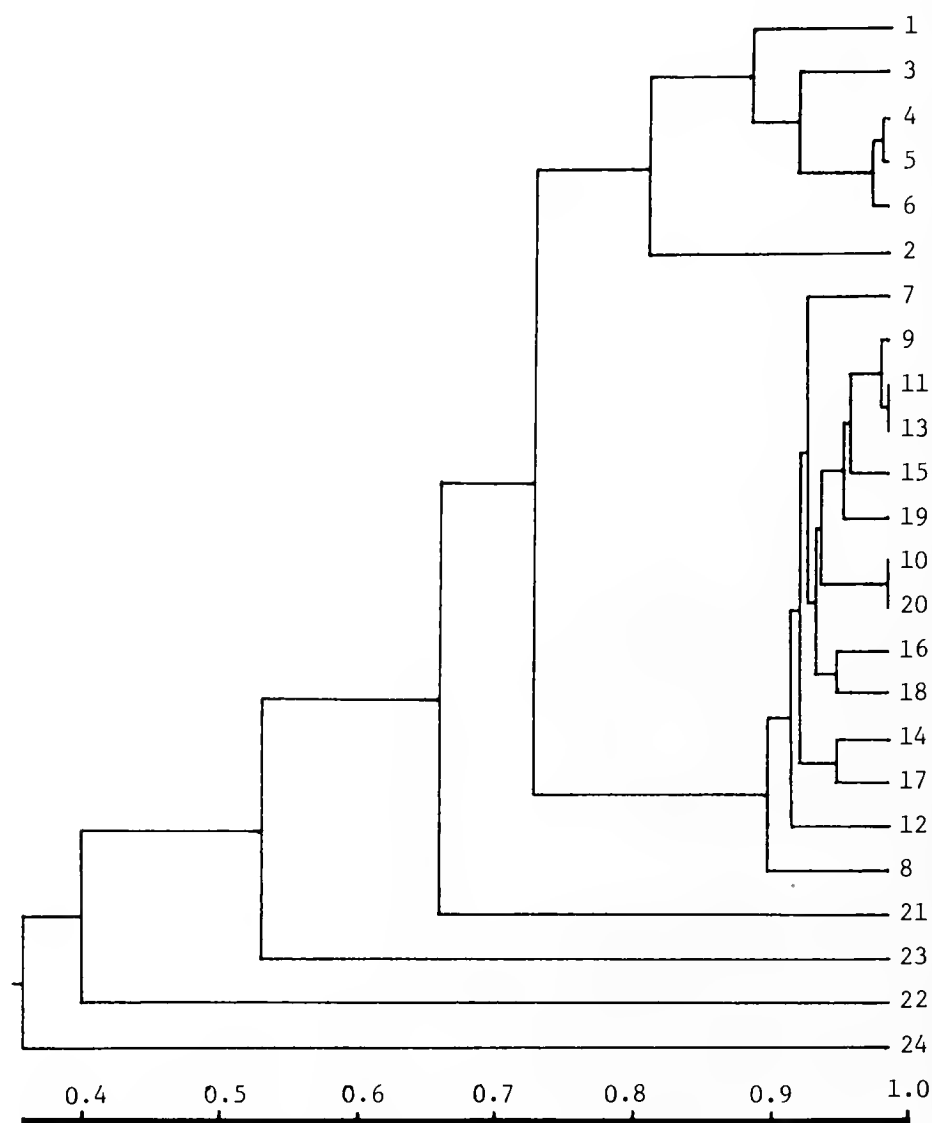
TABLE 22.—Allozyme frequencies for 15 loci for 24 numbered samples of glossophagine bats. Numbered samples (see text for key to sample numbers) represent five species of Glossophaga and four outgroup genera (Monophyllus, Leptoncycteris, Choeronycteris, and Lonchophylla).

Sample number	Mdh-1	Mdh-2	Ldh-1	Idh-1	Alb	Mpi	Pep-1	Pep-2	Pgm-1	Pgm-2	Ipo-2	Got-1	Got-2	Adh	α-Gpd
1	2	1	4	3	3(0.937) 2(0.063)	3	1	3(0.500) 1(0.500)	8(0.375) 5(0.625)	3(0.063) 2(0.937)	1	3	2	4(0.125) 2(0.875)	4(0.313) 3(0.687)
2	2	1	4	3	5(0.875) 3(0.125)	3	1	5(0.875) 3(0.125)	8	2	1	3	2	5	4(0.125) 3(0.875)
3	2	1	4	3	1	3	1	3	8(0.875) 5(0.125)	2	1	3	2	2	4
4	2	1	4	3	3(0.625) 2(0.375)	3	1	3	8	2	1	3	2	4(0.100) 2(0.900)	4
5	2	1	4	3	3	3	1	3	8	2	1	3	2	2	4
6	2	1	4	3	3(0.800) 2(0.200)	3	1	3	8	2	1	3	2	4(0.100) 3(0.400)	4
7	2	1	4	4(0.100) 3(0.700) 2(0.200)	3	3	2	5	3(0.350) 1(0.650)	2	1	3	2	2(0.500) 4(0.500) 2(0.500)	3
8	2	1	4	3	3	3	2	5(0.937) 3(0.063)	3	2	1	3	2	5(0.250) 4(0.625)	3
9	2	1	4	3	4(0.056) 3(0.944)	3(0.944) 2(0.056)	2	5	3	2	1	3	2	2(0.125) 6(0.111) 5(0.222) 4(0.445) 2(0.222)	3
10	2	1	4	3	3	3	2	5	3	2	1	3	2	2	3
11	2	1	4	3	3	3(0.050) 2(0.950)	2	5	3(0.900) 1(0.100)	2	1	3	2	5(0.100) 4(0.300) 2(0.600)	3
12	2	1	4	3(0.750) 2(0.250)	3	5(0.250) 3(0.750)	3(0.500) 2(0.500)	5	3	2	1	3	2	4(0.500) 2(0.500)	3

TABLE 22.—Continued.

Sample number	Mdh-1	Mdh-2	Ldh-1	Idh-1	Alb	Mpi	Pep-1	Pep-2	Pgm-1	Pgm-2	Ipo-2	Got-1	Got-2	Adh	α-Gpd
13	2	1	4	3	3	3	2	5	3	2	1	3	2	5(0.250) 4(0.250) 2(0.500)	3
14	2	1	4	3(0.900) 2(0.100)	3	3	2	5	5(0.200) 3(0.600) 1(0.200)	2	1	3	2	5(0.500) 4(0.500)	3
15	2(0.950) 1(0.050)	1	4	4(0.100) 3(0.750) 2(0.100) 1(0.050)	3	5(0.050) 3(0.950)	3(0.100) 2(0.900)	5	3(0.950) 1(0.050)	2(0.950) 1(0.050)	1	3	2	5(0.200) 4(0.400) 2(0.400)	3
16	2	1	4(0.750) 3(0.250)	3(0.625) 2(0.250) 1(0.125)	3	3	2	5	3(0.875) 1(0.125)	2	1	3	2	5(0.250) 4(0.250) 3(0.250) 2(0.250)	3
17	2	1	4	3	3	3(0.500) 2(0.500)	2	5	3	2	1	3	2	5(0.500) 4(0.500) 5(0.333) 2(0.667)	3
18	3(0.083) 2(0.917)	1	4(0.833) 3(0.167)	3(0.750) 2(0.250)	3	3	3(0.167) 2(0.833)	5	3(0.833) 1(0.167)	2	1	3	2	4(0.500) 2(0.500)	3
19	2	1	4	3(0.875) 2(0.125)	3	3	2	5	3	2	1	3	2	4(0.125) 3(0.875)	3
20	2	1	4	3(0.750) 2(0.250)	3	3	2	5	3	2	1	3	2	2	3
21	2	1	4	1	7	4	3	6	4	2	1	3	2	1	3
22	2	2	4	4	6	5	3	4	2	2	1	2	3	8	2
23	2	1	1	6	4	5	3(0.500) 2(0.500)	5	7	2	3	3	2	7	2(0.500) 1(0.500)
24	2	1	1	5	1	1	1	2	6	2	2	1	1	1	5

FIG. 30.—Similarity phenogram for 24 samples of glossophagine bats based on allozyme data. This phenogram is from the matrix of Rogers' *S*-values (Table 21) for five species of *Glossophaga* and four outgroup genera (see text for key to sample numbers). The coefficient of cophenetic correlation for this phenogram is 0.989.



Grenadines (Carriacou Island); the genic data for these individuals, therefore, were lumped into one sample (5).

Levels of genic heterozygosity and polymorphism are shown in Table 23 for 17 loci in the five species of *Glossophaga*. No heterozygosity was found in the sample of *G. morenoi* (Chiapas), one sample of *G. longirostris* (Carriacou Island and Venezuela combined), or two samples of *G. soricina* (western Perú and Venezuela). Overall, *G. leachii* was the most heterozygous species ($H=0.0515$), but heterozygosity in *G. soricina* from Sonora was highest for a single population ($H=0.1176$). Approximately 65 percent of the loci examined were polymorphic across all populations of *G. soricina*; individual populations varied in polymorphic loci from zero to approximately 41 percent. Levels of polymorphism averaged lowest in *G. morenoi* (approximately six percent) relative to the other four species. The data herein presented for *G. soricina* agree well with those of Straney *et al.* (1979), who examined genic variability in one population of *G. soricina* from Trinidad and found average heterozygosity to be 0.018 with one of 17 loci (approximately six percent) polymorphic.

Specimens used in the electrophoretic study, localities followed by sample size in parentheses, are listed below. *Glossophaga leachii* (sample 1): México, Chiapas,

TABLE 23.—*Biochemical variability in five species of Glossophaga. H is the average heterozygosity, and P is the percent of polymorphic loci. See text for key to sample numbers.*

Sample Number	N	H	P
1	8	0.0515	35.29
2	4	0.0441	17.65
3	8	0.0000	5.88
4	10	0.0353	11.76
5	11	0.0000	0.00
6	10	0.0117	11.76
4-6	31	0.0157	11.76
7	10	0.0529	17.65
8	8	0.0074	11.76
9	9	0.0131	17.65
10	1	0.0000	0.00
11	10	0.0000	17.65
12	2	0.1176	23.53
13	2	0.0294	5.88
14	5	0.0706	17.65
15	10	0.0647	41.18
16	4	0.0735	23.53
17	2	0.0588	11.76
18	6	0.0588	35.29
19	4	0.0294	17.65
20	2	0.0294	5.88
7-20	75	0.0433	64.71
1-20	126	0.0309	64.71

8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa (8). *Glossophaga commissarisi* (sample 2): México, Chiapas, 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa (2), and 23.6 mi. N Huixtla, Hwy. 200 (2). *Glossophaga morenoi* (sample 3): México, Chiapas, 8.2 mi. SE, 2.5 mi. E Tonalá, Río Ocuilapa (8). *Glossophaga longirostris*: (sample 4) Union Island, 0.5-1.0 km. N Clifton (10); (sample 5) Carriacou Island, Craigston Estate (10), and Venezuela, Guárico, Hato Masaquaral, 45 km. S Calabozo (1); (sample 6) Grenada, St. George, Chemin River, 0.5 km. E Confer (10). *Glossophaga soricina*: (sample 7) Jamaica, St. Ann, Green Grotto (10); (sample 8) Bolivia, La Paz, 1 mi. N Puerto Linares, Tomonoco (8); (sample 9) Suriname, Nick-erie, Kayserberg airstrip (9); (sample 10) Perú, Lambayeque, 0.5 km. N Rafan, 3 m., (1); (sample 11) Venezuela, Guárico, Santa Crucita Campground, Parque Nacional Guatopo (10); (sample 12) México, Sonora, Minas Nuevas, 4 mi. NW Alamos, (2); (sample 13) México, Sinaloa, 2 mi. NE Rosario, rd. to Matatán (2); (sample 14) México, Nayarit, 0.4 mi. E Acaponeta, Hwy. 15 (5); (sample 15) México, Guerrero, 24.1 mi. N Río La Unión, Hwy. 200 (10); (sample 16) México, Tabasco, 26.9 mi. W, 1.8 mi. S Villahermosa (4); (sample 17) México, Veracruz,

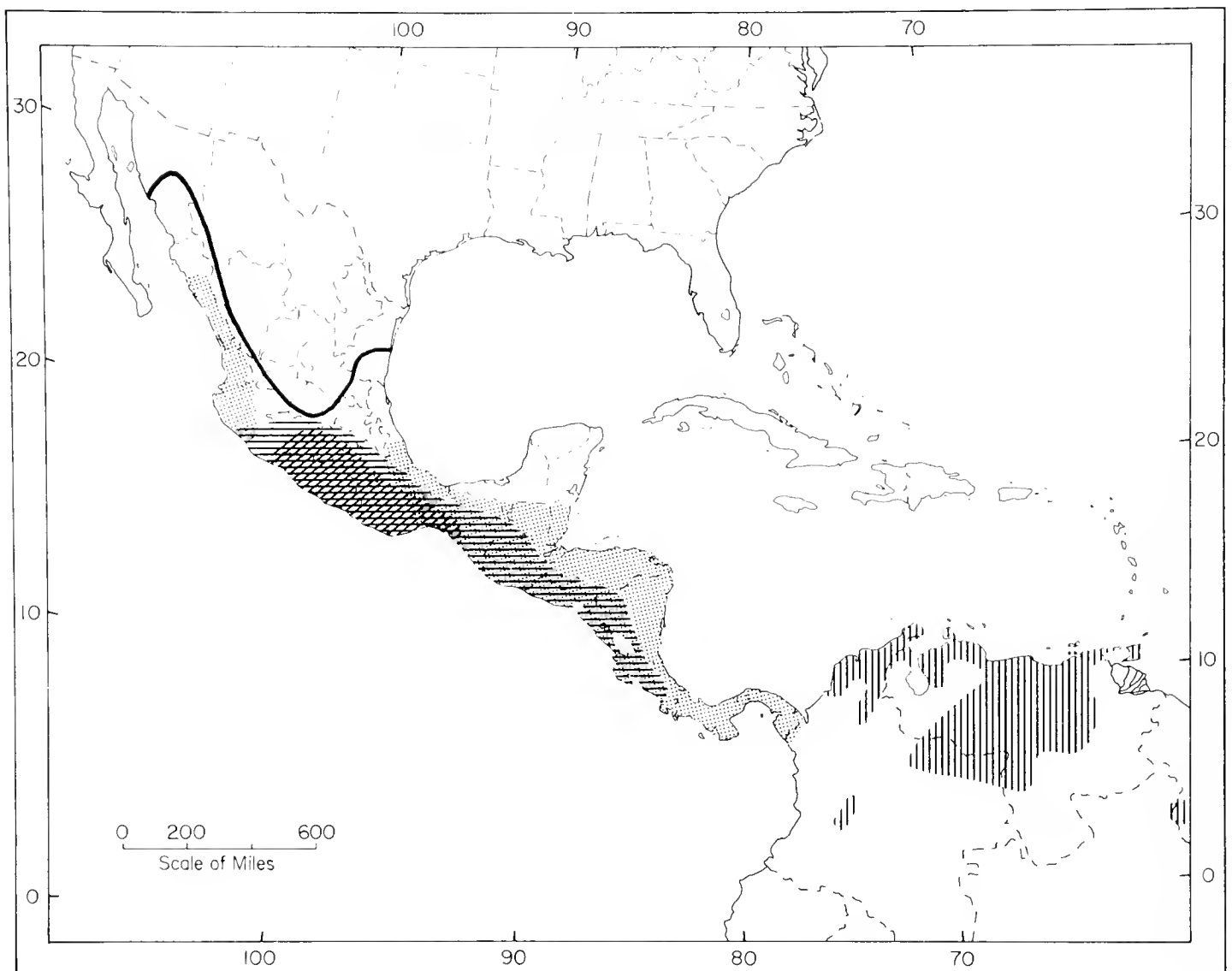


FIG. 31.—Geographic distribution of five species of *Glossophaga* on mainland North America and northern South America, showing areas of sympatry. *Glossophaga soricina* occurs throughout the mainland south of the solid line; *G. longirostris* is distributed in northern South America (vertical lines); *G. commissarisi* occurs in western México and again from southern México to Panamá (stipple); *G. leachii* is known from western México to Costa Rica (horizontal lines); and *G. morenoi* is confined to southwestern México (diagonal lines). See text for discussion.

Ojo de Agua, Río de Atoyac (2); (sample 18) México, Oaxaca, 11.0 mi. N Matias Romero (3), and 1.7 mi. S Matias Romero (3); (sample 19) México, Chiapas, 1 mi. S Tuxtla Gutiérrez (4); (sample 20) México, Yucatán, Mérida, Club Campestre (2). *Monophyllus plethodon* (sample 21): Dominica, St. Paul, Springfield (1). *Leptonycteris curasoae* (sample 22): México, Sonora, Minas Nuevas, 4 mi. NW Alamos (1). *Choeronycteris mexicana* (sample 23): México, Sonora, 8 mi. S Alamos (1). *Lonchophylla thomasi* (sample 24): Bolivia, La Paz, 1 mi. W Puerto Linares, Tomonoco (1).

Distribution

Bats of the genus *Glossophaga* are distributed from México (Sonora in the west and Tamaulipas in the east) southward throughout most of South America to Paraguay and northern Argentina; insular populations are known from the Tres

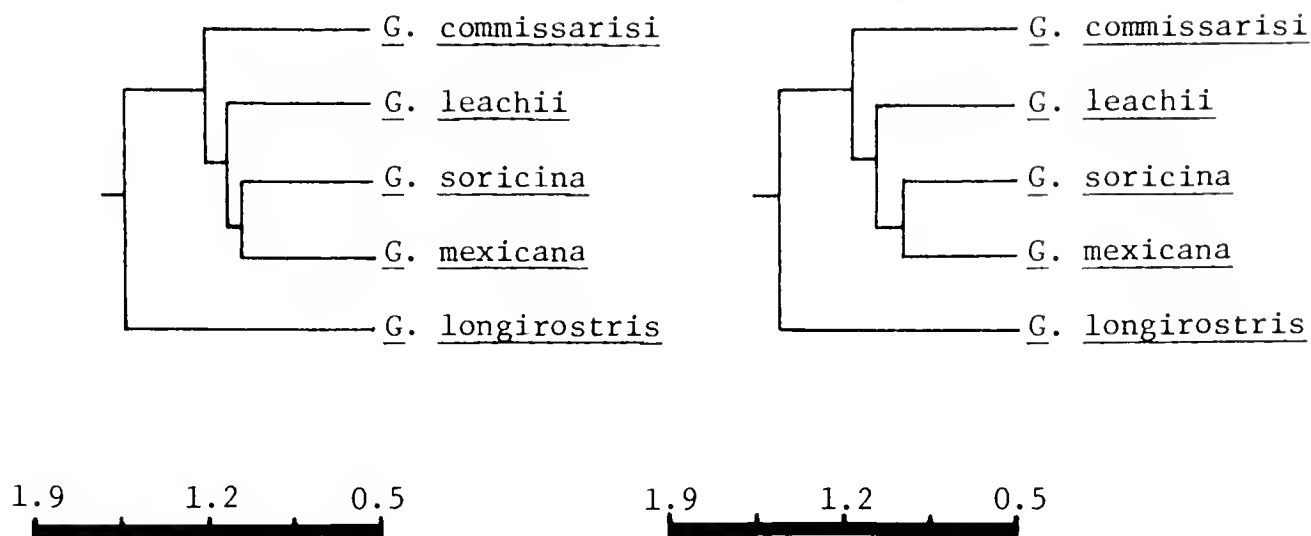


FIG. 32.—Distance phenogram for five species of *Glossophaga* based on morphological data. Phenograms were computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages for males (left) and females (right). The cophenetic coefficient of correlation for the phenogram for males is 0.817 and for females is 0.809.

Marías Islands, Jamaica, and the islands immediately adjacent to northern South America (including the Lesser Antilles as far north as St. Vincent). *G. soricina* is by far the most widespread species of the genus, occurring throughout all of the range of *Glossophaga* except some of the Caribbean Islands (where only *G. longirostris* is known). The ranges of *G. commissarisi*, *G. leachi*, and *G. morenoi* are included entirely within that of *G. soricina*.

The geographic distribution of *G. commissarisi* is fragmented into three disjunct ranges: western México from Sonora southward to Colima; southern México (Veracruz, Oaxaca, and Chiapas) and Belize southeastward at least to Panamá; and the upper Amazon Basin. *G. commissarisi* has been taken with *G. soricina* in each of these areas (Baker, 1967; Davis *et al.*, 1964; Dickerman *et al.*, 1981; Gardner, 1962; Handley, 1966; Hellebuyck *et al.*, 1985; Howell and Burch, 1974; Jones, 1966; Jones, *et al.*, 1972; LaVal, 1970; Webster and Jones, 1983). Also, the ranges of *G. leachii* and *G. morenoi* partially overlap that of *G. commissarisi* and are discussed below.

Glossophaga leachii is distributed continuously along the Pacific versant from western México (Colima and Jalisco) southeastward to central Costa Rica. The range of *G. leachii* is entirely within that of *G. soricina* and both species have been taken at the same localities (Dickerman *et al.*, 1981; Gardner, 1962; Jones, 1966). *G. leachii* is also sympatric with *G. commissarisi* from southern México southeastward to Costa Rica, and they too have been collected at localities with and without *G. soricina* (Dickerman *et al.*, 1981).

Glossophaga longirostris and *G. soricina* are sympatric in much of northern South America (Colombia, Venezuela, Trinidad, and Guyana), and both species have been captured together at many localities (J. A. Allen, 1900, 1911; Handley, 1976; Hershkovitz, 1949; Pirlot and León, 1965; Robinson and Lyon, 1901; Tamsitt and

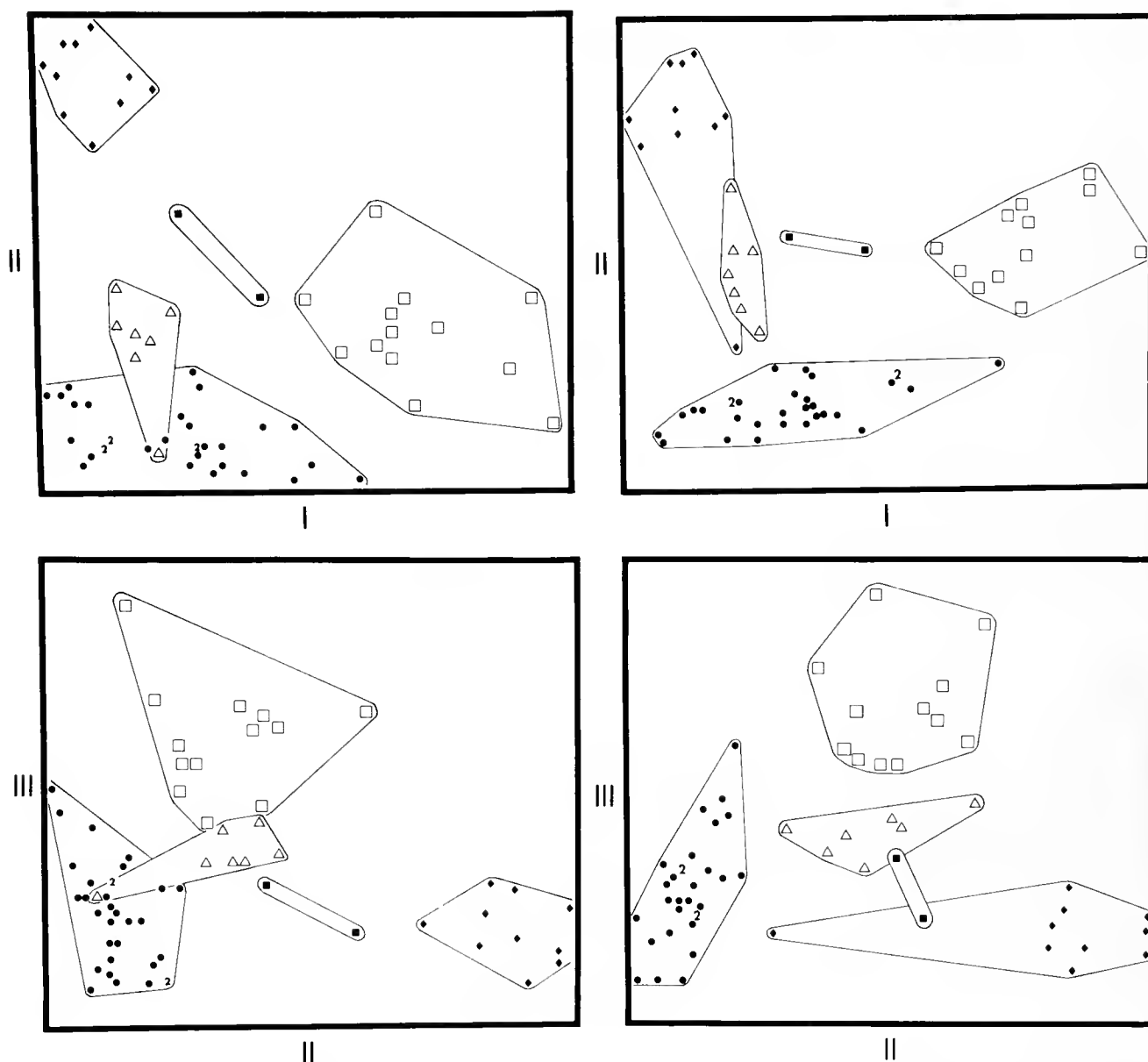


FIG. 33.—Two-dimensional plots for 64 samples of *Glossophaga* analyzed. Diamonds, triangles, large open squares, small solid squares, and circles represent samples of *G. commissarisi*, *G. leachii*, *G. longirostris*, *G. morenoi*, and *G. soricina*, respectively. Top, component I plotted against component II for males (left) and females (right); bottom, component II plotted against component III for males (left) and females (right).

Valdivieso, 1963; Valdivieso, 1964). The ecological preferences of these species have been fairly well documented in Venezuela (Handley, 1976), however, and *G. longirostris* usually inhabits xeric lowlands whereas *G. soricina* is more common in mesic sylvan environments. For example, both species occur in the relatively dry upper Magdalena River Valley and northern coast of Colombia, but only *G. soricina* is distributed continuously throughout the humid forests in the intervening Magdalena Valley. *G. longirostris* has invaded most of the arid islands immediately adjacent to northern South America, from some of which *G. soricina* is not known. *G. longirostris* is not sympatric with *G. commissarisi*, *G. leachii*, or *G. morenoi* based on current records of capture.

The known range of *G. morenoi* includes Michoacán, Morelos, Puebla, Guerrero, Oaxaca, and Chiapas; it occurs completely within the geographic distributions of *G. leachii* and *G. soricina*, and partially overlaps that of *G. commissarisi* (in eastern

TABLE 24.—Factor loadings for 26 characters examined in five species of Glossophaga. Only loadings above 0.600 (or below -0.600) on the first four principal components are shown (males above, females below).

Character	I	II	III	IV
Length of forearm			0.600 0.831	
Length of third metacarpal			0.760	
Length of fourth metacarpal			0.794	
Length of fifth metacarpal			0.600 0.765	
Greatest length of skull	0.872 0.841			
Condylobasal length	0.864 0.845			
Zygomatic breadth			0.738 0.772	
Length of rostrum	0.879 0.875			
Mastoid breadth			0.826 0.828	
Interorbital breadth	0.730 0.643			
Breadth of braincase			0.894 0.912	
Depth of braincase			0.946 0.919	
Length of maxillary toothrow	0.849 0.851			
Length of mandibular toothrow	0.845 0.858			
Width across molars	0.689		0.630	
Mandibular length	0.795 0.810			
Pelage coloration				0.792
Pterygoid alae		-0.800 -0.793		
Presphenoid ridge		-0.856 -0.821		
Lower incisors		-0.862 -0.805		
Upper incisor angle	-0.600	0.660 0.700		
Upper incisor size		0.683 0.793		

TABLE 24.—Continued.

Character	I	II	III	IV
Basisphenoid pits		0.625		
P3:P4 bulk				
Rostral slope	-0.918			
	-0.904			
Postpalatal processes				-0.805

Oaxaca and western Chiapas). I have taken all four species together near Tonalá, México (see also Gardner, 1962).

Glossophaga soricina has the largest geographic distribution of any glossophagine (see Koopman, 1981), and commensurately occupies more biotic provinces than other Neotropical long-tongued bat. It has successfully invaded Jamaica and the Tres Mariás Islands and also inhabits the arid Yucatán Peninsula, xeric west coast of Ecuador and Perú, and relatively dry slopes bordering the Mexican Plateau—all physiographic areas from which other congeners are unknown. *G. soricina* also occupies much of tropical South America east of the Andes, for the most part an area lacking other species of *Glossophaga*.

The patterns of distribution among the five species of *Glossophaga* broadly overlap (Fig. 31), particularly in southern México and Central America where three (and sometimes four) species are sympatric. If resources such as food or roost sites are in short supply in areas where sibling species are sympatric, then interspecific competition ostensibly is enhanced, and some mechanism that tempers this increased rivalry may occur. Character displacement is one process by which closely related species reduce interspecific competition. Among vertebrates, character displacement has best been documented in bill length in birds (for example, see Lack, 1947; MacArthur, 1958; Selander, 1966; Vaurie, 1951) and mating calls of anurans (for example, see Blair, 1955, 1958, 1974; Brown and Wilson, 1956; Fouquette, 1975; Jones, 1973; Littlejohn, 1960, 1965; Littlejohn and Loftus-Hills, 1968; Loftus-Hills, 1975; Mechum, 1961; Watson and Martin, 1968). Graham and Semken (1976) thought allometric character displacement to be responsible for the comparatively large, medium, and small sizes of *Blarina brevicauda*, *B. [brevicauda] kirklandi*, and *B. carolinensis*, respectively, which facilitated their divergence from a common ancestor, hence their predominantly parapatric distributions in the eastern United States. There is scant evidence that demonstrates if and how character displacement reduces interspecific competition in bats.

In parameters examined by me, character displacement is evident in at least two species of *Glossophaga* that inhabit Middle America. Four species of the genus

Character		<i>commissarisi</i>	<i>leachii</i>	<i>longirostris</i>	<i>morenoi</i>	<i>soricina</i>
7	M1 parastyle	1	1	1'	1'	0
6	presphenoid ridge	1	0	0	1	0
5	pterygoid alae	1	0	2	1	0
4	lower incisors	2	1	0	1'	0
3	rostral slope	0	0	1	1	0
2	P3:P4 bulk	0	0	1	1	0
1	mandibular sym- physeal ridge	0	0	1	1	0

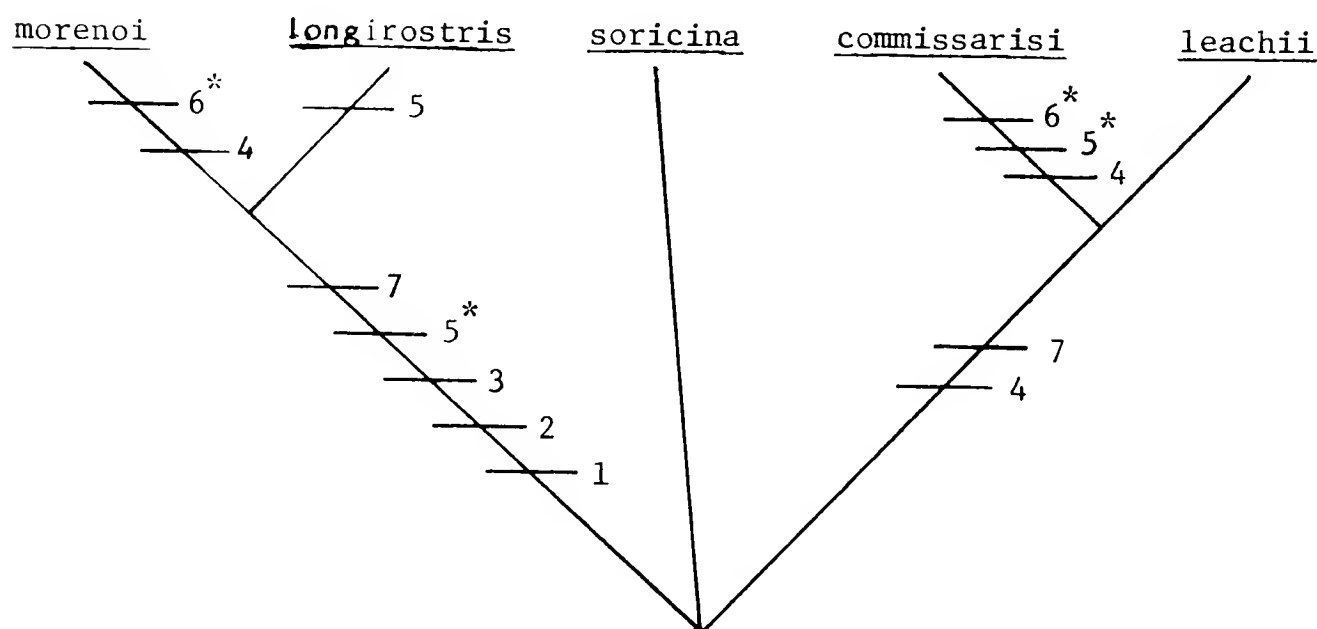
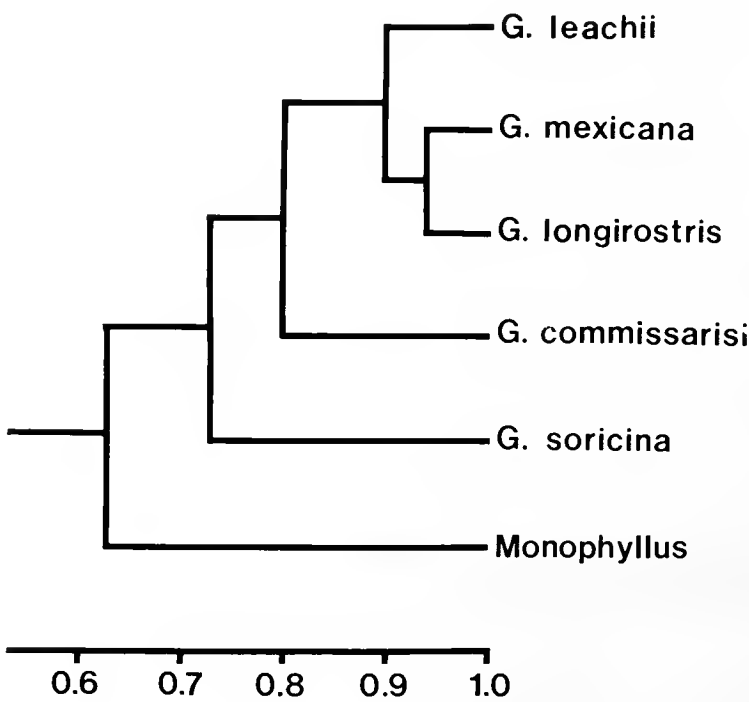


FIG. 34.—Cladistic relationships among five species of *Glossophaga* using qualitative cranial characters. Characters are coded as plesiomorphic (0) or apomorphic (1', 1, and 2); evolutionary direction is from 0 to 1 (to 2), or 0 to 1'. Asterisks indicate assumed convergence in character states.

have been taken together along the Pacific versant at the Isthmus of Tehuantepec, an area characterized by xeric thorn forest with small patches of tropical deciduous and evergreen forest along streams and rivers. Here, *G. morenoi mexicana* averages much larger than sympatric congeners and *G. m. morenoi* (a race of *G. morenoi* yet to be taken with other congeners) in many external and most cranial dimensions. Furthermore, the pelage of *G. m. mexicana*, in contrast to that of *G. m. morenoi* and all other species of *Glossophaga*, is more distinctly bicolored in this area of sympatry.

Another species, *G. commissarisi*, also exhibits character displacement in areas where it is sympatric with *G. soricina handleyi* and, in part, *G. leachii* and *G. morenoi mexicana*. In specimens of *G. c. commissarisi* from eastern México southeastward to Panamá, the pelage is distinctly darker and the rostrum averages

FIG. 35.—Rogers' similarity phenogram for five species of *Glossophaga* using *Monophyllus* as an outgroup. The coefficient of cophenetic correlation is 0.989 for this phenogram.

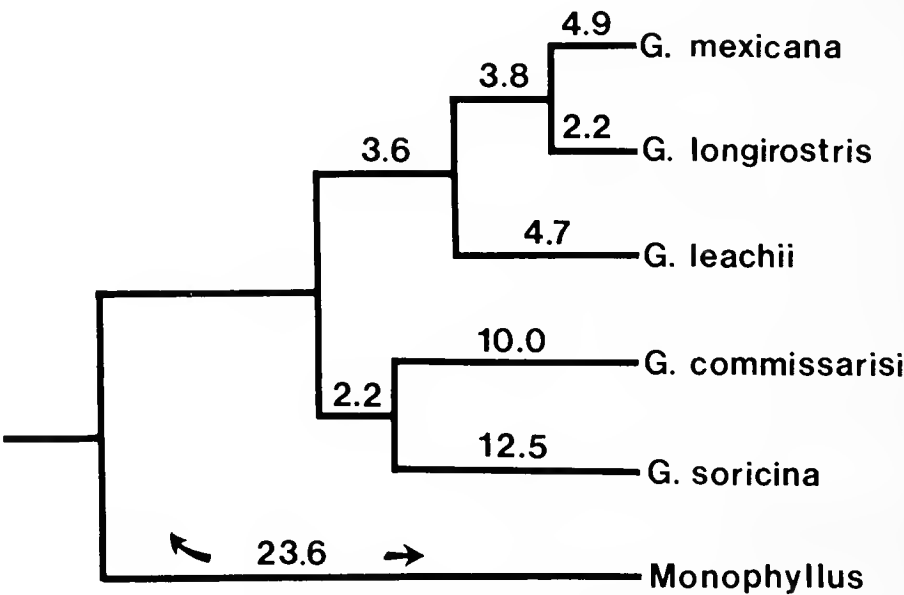


smaller than sympatric congeners. On the other hand, specimens of *G. c. hespera* and *G. c. bakeri*, presently known only to be sympatric with *G. s. handleyi* and *G. s. soricina*, respectively, most closely resemble individuals of *G. soricina* in both characters.

EVOLUTION OF THE GENUS *GLOSSOPHAGA*

Several aspects of cranial, dental, hair, chromosomal, and biochemical morphology, as well as the current patterns of distribution among the five species of *Glossophaga*, were compared in the previous chapter. Morphology of hair and chromosomes contributes little to understanding the relationships among the species, and is, therefore, omitted from further discussion. Phenograms or cladograms, or both, were generated from each remaining data set; the following discussion is based on these composite data. Unfortunately the fossil record for

FIG. 36.—Fitch-Margoliash phylogenetic tree for five species of *Glossophaga* using *Monophyllus* as an outgroup. The *F*-value for this tree is 8.35 percent.



glossophagines is extremely depauperate, but it does establish a useful frame of reference timewise.

Quantitative, qualitative, and pelage coloration data were analyzed together using NT-SYS programs. Phenograms generated from these data for male and female samples of *Glossophaga* are similar; distance phenograms are included herein (Fig. 32) because they have higher coefficients of cophenetic correlation. Specimens of *G. morenoi* and *G. soricina* most closely resemble each other phenetically; this similarity probably is responsible for most specimens of *G. morenoi* having been misidentified as *G. soricina* before this investigation was initiated. *G. morenoi* and *G. soricina* are similar in overall size and in the procumbent nature of the upper incisors. In the phenogram, specimens of *G. leachii* cluster tightly with those of the *morenoi-soricina* complex, and then individuals of *G. commissarisi* group with the other Middle American species. Lastly, bats referable to *G. longirostris* least resemble other species of *Glossophaga* phenetically.

The first four principal components were computed from the correlation matrix among the 26 characters for all samples for the five species of *Glossophaga* for both males and females. The first four principal components combine to express 83.8 percent of the phenetic variation in males and 85.1 percent in females. The amount of phenetic variation represented in the first four principal components for males and females, respectively, was 53.6 and 53.5 for component I, 16.4 and 16.8 for component II, 9.4 and 9.5 for component III, and 4.4 and 5.3 for component IV. Two-dimensional plots of principal component I-II and II-III are presented for both sexes (Fig. 33). Characters with loadings above 0.60 (or below -0.60) on any of the first four principal components are shown in Table 24.

The two-dimensional plots of male and female *Glossophaga* are similar. OTUs on the right-hand side of component I are larger than average for the genus in measurements of cranial length, interorbital breadth, and have a gradual rostral slope; this includes all samples of *G. longirostris* and the large races of *G. soricina* (*antillarum*, *mutica*, and *valens*). OTUs on the left-hand side of component I, including all samples of *G. commissarisi*, *G. leachii*, and *G. s. soricina*, are smaller than average in these measurements and have a pronounced rostral slope. Some qualitative characters load heavily on component II such that OTUs to the top of this component (samples of *G. commissarisi*) lack pterygoid alae and a presphenoid ridge, possess small lower incisors, and have decumbent upper incisors, the outer pair frequently larger than the inner in bulk. OTUs to the bottom of component II (samples of *G. soricina*) are opposite in these characters. In the two-dimensional plots of principal components II-III, OTUs to the top of component III are larger than average for the genus in measurements of the wing and cranial breadth and depth. This includes all samples of *G. longirostris* and the large races of *G. soricina* (*antillarum*, *mutica*, and *valens*). The relatively large wing measurements of *G. leachii* also are clearly evident on this component. The relatively distant OTU of female *G.*

commissarisi and male *G. leachii* are sample localities that were represented by single specimens; species clusters are well separated if these two individuals are ignored. Plots of component I-III, I-IV, and III-IV are essentially linear, and the OTUs for each species broadly overlap, thus demonstrating the allometric relationships between the species of *Glossophaga*. Size alone, therefore, is not a useful tool to distinguish among the species.

Several qualitative characters were determined to be plesiomorphic (primitive) or apomorphic (derived) for each species of *Glossophaga* based on critical comparisons with outgroups (other glossophagine genera and *Micronycteris*), and a cladistic analysis was performed on these data. The resulting cladogram (Fig. 34), an unresolved trichotomy, reveals that *G. longirostris* and *G. morenoi* share five synapomorphies—an absent or poorly developed mandibular symphyseal ridge, subequal or equal upper premolars, an elongate rostrum, and the loss of pterygoid alae and the parastyle of M1. The second clade includes *G. soricina* and is plesiomorphic for all cranial characters examined by me. Two synapomorphies (reduced lower incisors, and the reduced parastyle of M1 that is directed labially to posterolabially for the paracone) unite the members of the third clade, *G. commissarisi* and *G. leachii*. Two homoplasies (reversals or convergence, but the latter is more parsimonious in this example) are evident: pterygoid alae have been lost in *G. commissarisi*, *G. longirostris*, and *G. morenoi*; and the presphenoid ridge is subterminally flattened in both *G. commissarisi* and *G. morenoi*. It is of note that the presence or absence of a complete presphenoid ridge also discriminates between specimens of *Leptonycteris nivalis* and *L. curasoae*.

Another point of interest is that I consider the reduced and evenly-spaced lower incisors of *G. morenoi* to have evolved independently from the reduced and paired lower incisors of the *commissarisi-leachii* clade. Nectar-feeding bats generally have lower incisors that are modified in such a way as to facilitate tongue movement when feeding. Two common modifications are the reduction in size of the teeth and pairing of the teeth. The lower incisors of *G. morenoi* are reduced in size without subsequent pairing. The lower incisors of *G. commissarisi* and *G. leachii*, on the other hand, clearly are paired; and the reduction in size is apparently a secondary modification. Similarly, the reduced parastyle of M1 that is directed labially to posterolabially from the paracone in *G. commissarisi* and *G. leachii* is considered by me to be a separate event not related to the total loss of the M1 parastyle in *G. longirostris* and *G. morenoi*.

The genic data provide yet another phenogram (Fig. 35) based on Rogers' *S*-values. Specimens of *G. longirostris* and *G. morenoi* are closest biochemically; next, individuals of *G. leachi* join this complex; finally, specimens of *G. commissarisi* and then *G. soricina* join the *leachii-longirostris-morenoi* complex. A Fitch-Margoliash (1967) phylogenetic tree (Fig. 36) was constructed from Rogers' *D*-values, and the specific relationships were similar to those of the similarity

phenogram except that *G. commissarisi* and *G. soricina* more closely resemble each other biochemically than either does bats of the *leachii-longirostris-morenoi* complex. Another approach frequently used to interpret allozyme data is to employ a cladistic analysis using each locus as a distinct character. However, only two loci had fixed allele differences between the species (one for *G. morenoi* and the other for *G. soricina*), so this approach does little to resolve the affinities among the species, as was the case with the species of *Dermanura* examined by Koop and Baker (1983).

Bats of the genus *Glossophaga* are distributed throughout the New World tropics, but patterns of endemism indicate that southern México may well be the center of radiation from a common ancestor. It is, however, impossible to test this hypothesis, and a South American origin with a subsequent invasion of Central America is a possible alternative. Regardless, fossils of *Glossophaga soricina* have been collected from sub-Recent deposits in several caves in Yucatán, México (Hatt *et al.*, 1953), and those of *G. longirostris* (reported as *G. soricina*) have been taken from sub-Recent deposits in Aragua, Venezuela (Linares, 1968). The endemic Antillean genus *Monophyllus* is undoubtedly derived from a *Glossophaga longirostris* ancestor (Koopman, 1981), and fossils of the former are known from the late Pleistocene of Cuba (Koopman and Ruibal, 1955; Silva Taboada, 1974), Jamaica (Williams, 1952), Puerto Rico (Anthony, 1917, 1918; Choate and Birney, 1968; Reynolds *et al.*, 1953), and the sub-Recent of Haiti (Miller, 1929). The two genera obviously were distinct prior to the late Pleistocene and occupied part, if not most, of their current geographic distributions at that time.

The phenograms and cladograms are not congruent, so it is difficult to ascertain the relationships among the five species. Quantitative data are usually poor indicators of specific identity, and, therefore, can be excluded from consideration. Likewise, the morphology of the enzymes is sufficiently similar to preclude its use as well. It appears that qualitative cranial features best explain the evolutionary relationships among the species of *Glossophaga*. With due consideration to the companion data sets, the following evolutionary scenario focuses on qualitative cranial characters, and suggests that the relatively rapid climatic and habitat changes that took place during the Quaternary are responsible for relationships.

Changes in climate and habitat during the Quaternary have greatly influenced the Recent flora and fauna of Central and South America (Vuilleumier, 1971). The model of Pleistocene refugial speciation (Haffer, 1969) has been shown to apply to various groups of plants (Morley, 1975; Prance, 1973; Simpson, 1975; Solbrig, 1976), *Drosophila* (Spassky *et al.*, 1971; Winge, 1973), butterflies (Brown, 1977a, 1977b; Brown *et al.*, 1974), fishes (Miller, 1966), amphibians (Lynch, 1979, and included citations), reptiles (Dixon, 1979, and included citations; Duellman, 1966; Rivero-Blanco and Dixon, 1979; Savage, 1966), birds (Haffer, 1974, and included citations, 1979), and many groups of mammals (Cerqueira, 1982, and included cita-

tions; Choate, 1970; Genoways, 1973). The gist of all the aforementioned studies is that alternating semiarid and wet climatic conditions during the Quaternary precipitated major changes in habitat. During dry periods, wet tropical forests receded into areas where there remained sufficient moisture and were replaced by savanna or open woodlands. Species adapted to a sylvan existence were restricted to these forest refugia, thereby providing each isolated population opportunity for differentiation. During wet periods the forests expanded; formerly isolated populations became more widespread, whereas savanna-adapted species had shrinking geographic distributions and eventually become isolated. This model has been independently supported by both palynological (van der Hammen, 1974; van der Hammen *et al.*, 1972) and geomorphological (see Simpson and Haffer, 1978, for citations and discussion) studies.

The results of this investigation indicate that the genus *Glossophaga* is comprised of three clades (Fig. 34). One includes *G. longirostris* and *G. morenoi*, the second includes *G. soricina*, and the third contains *G. commissarisi* and *G. leachii*. It is difficult to reconstruct the events leading to the trifurcation of these groups from a common ancestor, or to place this event geographically. Current ecological requirements indicate that *G. longirostris* and *G. morenoi* inhabit relatively xeric environments, whereas *G. commissarisi*, *G. leachii* and *G. soricina* usually occupy mesic and wet habitats. There are exceptions, however, for *G. soricina valens* has invaded the arid west coasts of southern Ecuador and Perú, and *G. s. handleyi* occurs on the relatively dry Yucatán Peninsula. Given these current ecological requirements, it appears that relatively rapid changes in climate caused this early trichotomy, the result being a more arid-adapted group (*G. longirostris* and *G. morenoi*), a more mesic-adapted group (*G. commissarisi* and *G. leachii*), and a third group (*G. soricina*) that probably occurred in habitats ranging from dry to wet. Throughout the climatic changes characteristic of the Quaternary Period, as the arid-adapted group expanded its geographic distribution, the mesic-adapted group retreated into restricted areas of suitable habitat.

During a warm, dry period the *longirostris-morenoi* lineage was widely distributed throughout Middle America and northern South America. A subsequent cool, wet period separated this group into two discrete populations. Today, *G. longirostris* is distributed throughout the xeric northern coast of South America and many of the adjacent Caribbean islands, whereas *G. morenoi* is restricted to the arid lowlands of southern México and the relatively dry slopes of the Sierra Madre del Sur, Sistema Montañoso, and Cordillera Volcánica.

The mesic-adapted group evolved in similar fashion, but the climate and habitat changes had the opposite effect on its geographic distribution. During a wet period the ancestor to *G. commissarisi* and *G. leachii* was widely distributed throughout Central America. A subsequent dry period then restricted the *commissarisi-leachii* ancestor into two isolated areas of suitable habitat, possibly central México (for *G.*

leachii) and Central America (for *G. commissarisi*). The climate today is relatively warm and wet. As a result, the geographic distributions of bats in this group broadly overlap in southern México and Central America.

Three interesting patterns of distribution deserve comment. *Glossophaga soricina* apparently invaded the Tres Mariás Islands and Jamaica during a cool period as sea levels were lowered during glacial maxima. For example, the sea level was lowered approximately 120 meters during maximum Illinoian glaciation (Gascoyne *et al.*, 1979). In all probability the Tres Mariás Islands were connected to the mainland, or separated only by a narrow channel, and even freshwater fish occur there (Nelson, 1899). Certainly *G. soricina* invaded Jamaica via overwater dispersal (Baker and Genoways, 1978), for even during glacial maxima the mainland and Jamaica never were connected. Likewise, *G. longirostris* (and to a lesser extent *G. soricina*) has invaded several islands immediately adjacent to northern South America. Although some of these continental islands undoubtedly were connected to the mainland during times with lowered sea levels, others were not connected. Overwater dispersal best explains this pattern of distribution as well.

The second point of interest is that *G. commissarisi* is represented by three disjunct races. Obviously *G. commissarisi* was more widespread during more favorable times, and changes in climate and vegetation have reduced the amount of suitable habitat for this species. *G. longirostris* also has disjunct populations, indicating that it too was more widely distributed when climatic conditions were comparatively favorable. Finally, *G. soricina valens* and *G. s. soricina* apparently do not intergrade in Perú where their ranges are essentially parapatric. Intergradation is evident, however, between *G. s. valens* and *G. s. handleyi* in southwestern Colombia and between *G. s. handleyi* and *G. s. soricina* in the Magdalena River Valley of central Colombia. In a geological sense, *G. s. valens* and *G. s. soricina* must be quite distantly related.

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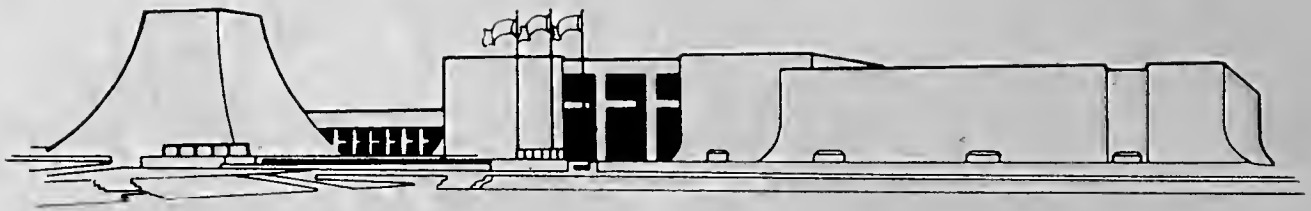
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Address of author: *Department of Biology, University of North Carolina, Wilmington, North Carolina 28403. Received 21 February 1991, accepted 24 June 1991.*



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ISBN 0-89672-260-9

SEP 25 1993

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MYOTIS EVOTIS
(CHIROPTERA: VESPERTILIONIDAE)**

Richard W. Manning

SPECIAL PUBLICATIONS, THE MUSEUM
TEXAS TECH UNIVERSITY
NUMBER 37
